University of Alberta

Plant-Herbivore Dynamics: Wapiti on Alfalfa Pastures

by

Ronald Lee Arthur ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of *Doctor of Philosophy*

Department of *Renewable Resources*

Edmonton, Alberta
Spring 2003

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisisitons et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-82078-5
Our file Notre référence
ISBN: 0-612-82078-5

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

Canada

University of Alberta

Library Release Form

Name of Author: *Ronald Lee Arthur*

Title of Thesis: *Plant-Herbivore Dynamics: Wapiti on Alfalfa Pastures*

Degree: *Doctor of Philosophy*

Year this Degree Granted: *2003*

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Box 3037, Vermilion, Alberta
T9X 2B1

Date: April 11, 2003

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Plant-Herbivore Dynamics: Wapiti on Alfalfa Pastures* submitted by *Ronald Lee Arthur* in partial fulfillment of the requirements for the degree of *Doctor of Philosophy*.

Dr. R.J. Hudson (co-supervisor)

Dr. J.R. King (co-supervisor)

Dr. R.J. Christopherson (committee member)

M. Anne Naeth

Dr. M.A. Naeth (committee member)

E.W. Bork

Dr. E.W. Bork (committee member)

Dr. K.M. Wittenberg (external examiner)

Date: April 10, 2003

In loving memory of my daughter,
Keltie Lee Arthur (1984 – 2000).

Keltie was a wonderful daughter, so full of love and life. She gave me happiness, hope, and a world of reasons to be proud. Her sudden death during the writing of this manuscript led me to deep sorrow and despair. But her memories remain and inspire me, to search for meaning and truth, to value life and living.

ABSTRACT

This study investigated farmed wapiti (*Cervus elaphus*) interactions with alfalfa (*Medicago sativa* L.) in Alberta, Canada. The first experiment compared wapiti-simulated defoliation (stripping) versus mowing at three heights on mid-vegetative alfalfa. Stripping alfalfa led to quicker recovery to a harvestable stand ($p<0.001$), but resulted in less regrowth ($p<0.05$), less total biomass ($p<0.001$), fewer crown-derived stems ($p<0.05$), and lower quality forage ($p<0.05$) than mowing. Recovery was three ($p<0.05$) and ten ($p<0.001$) days quicker for plants defoliated to a 15cm height than 7.5 and 2.5cm, respectively, but total biomass production ($p<0.05$) and forage quality ($p<0.01$) were lower for the tallest height. Regardless of treatment, the majority of post-treatment biomass was crown-derived rather than from axillary buds. Overall, mowing resulted in greater alfalfa quantity and quality but required longer stand recovery than stripping.

The second experiment focused on soluble root protein levels of alfalfa from April to October under four sward management systems (SMS) utilizing wapiti grazing and/or haying. Root protein levels were not different among SMS ($p>0.05$), but differed among sampling dates across SMS ($p<0.001$), decreasing during initial spring growth (April to early June), and increasing during late summer-fall (late August to October). Root protein levels were lower in October than April ($p<0.001$), but were adequate for subsequent growth initiation and not different ($p>0.05$) among SMS.

The third experiment examined wapiti feeding on pure alfalfa versus predominantly bromegrass (*Bromus riparius* Rehm. cv. Regar) pastures. In grass-dominated stands, estimated dry matter ($R^2=0.41$, $p<0.001$) and digestible energy ($R^2=0.39$, $p<0.01$) intake rates of wapiti were asymptotically related to available herbage, and superior to alfalfa-only stands at herbage levels below about 2500kg/ha. On pure alfalfa, dry matter ($R^2=0.81$, $p<0.001$) and digestible energy ($R^2=0.95$, $p<0.001$) intake rates fit a third order polynomial indicating wapiti foraging efficiency exceeded grass-dominated stands when herbage exceeded approximately 2500kg/ha.

Results of this study suggest graziers should consider grass:legume mixtures to maximize wapiti intakes over the widest range of available herbage, or, if managing pure alfalfa, consider short durational grazing and/or alternating hay cuts to foster abundant quality regrowth.

ACKNOWLEDGEMENTS

I wish to graciously thank my co-supervisors, Dr. Bob Hudson and Dr. Jane King, for their help, kindness, support and guidance. Dr. Hudson's eternal optimism, positive attitude, and scientific genius originally attracted me to perform this study. Dr. King taught me a great deal about forage physiology, and her vision and patience was absolutely integral to successful completion of this work. I am very thankful for the efforts and support of these two special people. They are consummate professionals.

I would also like to thank Dr. Anne Naeth and Dr. Ed Bork for their insightful editorial comments and guidance in development and completion of the thesis, and for their challenging analysis of the thesis as members of my examining committee. I also wish to thank Dr. Karin Wittenberg for her constructive criticism of the thesis. Her input resulted in a document with greater clarity and helped me advance my understanding of the thesis subject matter. Also, I wish to thank Dr. Bob Christopherson for his contributions to the thesis examining committee, and to Dr. Art Bailey and Dr. Bob Hardin for their wisdom and guidance in the planning and early stages of this study.

I also wish to thank Dr. Walter Dixon for his guidance in choosing appropriate methods for analysis of various plant samples in this study. Accordingly, I want to thank Joan Turchinsky for her leadership role in conducting the bulk of these analyses in a very competent and gracious manner. They are great people to work with! Also, thanks to Dick Purveen for his support in providing access to the Ellerslie farm facilities for grinding and preparation of forage samples, and to Gerry Ahlgren for his help in the field with the first experiment.

I also wish to thank Norwest Labs for supporting this research through their Agricultural Research Program, and to Ken Mrazek and Doug Keyes for their guidance in selecting appropriate analytical methods for the forage samples analyzed at Norwest Labs.

Finally, and most importantly, I want to thank my family for their help, love, and patience. A special thanks is in order for my children, Jim and Brigit, who, alongside my late daughter, Keltie, helped me perform the field research in this study. And to my wife, Kerri, who supported me unfailingly through this entire endeavor, I give my heartfelt thanks. To her, and to Jim and Brigit, I am forever indebted for the family time sacrificed during this study.

TABLE OF CONTENTS

1.0 INTRODUCTION 1
1.1 Historical Background 1
1.2 Industry Overview and Research Rationale 1
1.3 Wapiti Feeding Strategies 3
1.4 Research Objectives 4
1.5 References 6
2.0 REGROWTH IN VARIABLY DEFOLIATED ALFALFA 9
2.1 Introduction 9
2.2 Materials and Methods 10
2.2.1 Experimental Area 10
2.2.2 Climatological Data 11
2.2.3 Experimental Design 13
2.2.4 Pre-Treatment Monitoring 13
2.2.5 Treatment Application 13
2.2.6 Post-treatment Monitoring 15
2.2.7 Post-treatment Harvesting 15
2.2.8 Chemical Analyses 16
2.2.9 Statistical Analyses 16
2.3 Results 17
2.3.1 Regrowth Period 17
2.3.2 Regrowth and Total Herbaceous Biomass 17
2.3.3 Primary and Secondary Stem Density 18
2.3.4 Height of Origin of Secondary Stems 19
2.3.5 Forage Quality 20
2.4 Discussion 21
2.4.1 Regrowth Period 21
2.4.2 Regrowth and Total Herbaceous Biomass 21
2.4.3 Primary and Secondary Stem Density 22
2.4.4 Height of Origin of Secondary Stems 23
2.4.5 Forage Quality 23
2.4.6 Residual Biomass 24
2.5 Conclusions 25
2.6 References 26
3.0 EFFECT OF SWARD MANAGEMENT SYSTEMS ON ALFALFA REGROWTH POTENTIAL 30
3.1 Introduction 30
3.2 Materials and Methods 32
3.2.1 Experimental Area 32
3.2.2 Climatological Data 32
3.2.3 Experimental Design and Treatments 34
3.2.4 Available Herbaceous Biomass 35
3.2.5 Root Tissue Sampling 36
3.2.6 Chemical Analyses 37
3.2.7 Statistical Analyses 37

3.3 Results 38
3.3.1 Available Herbaceous Biomass 38
3.3.2 Soluble Root Protein 38
3.3.3 Root TNC and Soluble Protein Entering Dormancy 44
3.3.4 White Crown Bud Density 44
3.4 Discussion 45
3.4.1 Soluble Root Protein 45
3.4.2 Root TNC 49
3.4.3 White Crown Bud Density 49
3.5 Conclusions 50
3.6 References 51
4.0 FORAGING EFFICIENCY OF WAPITI ON TAME PASTURE 55
4.1 Introduction 55
4.2 Materials and Methods 55
4.2.1 Experimental Area and Animals 55
4.2.2 Experimental Design 57
4.2.3 Foraging Behavior and Available Herbaceous Biomass 58
4.2.4 Chemical Analyses and Nutritional Intake Rates 59
4.2.5 Statistical Analyses 59
4.3 Results 60
4.3.1 Forage Removals and Available Herbage 60
4.3.2 Dry Matter Intake Rate 60
4.3.3 Bite Size 61
4.3.4 Bite Rate 64
4.3.5 Nutritional Intake Rate 65
4.4 Discussion 66
4.4.1 Forage Removals and Available Herbage 66
4.4.2 Dry Matter Intake Rate 68
4.4.3 Bite Size 68
4.4.4 Bite Rate 70
4.4.5 Nutritional Intake Rate 70
4.5 Conclusions 71
4.6 References 72
5.0 SUMMARY DISCUSSION AND CONCLUSIONS 74
5.1 Experiments Performed 74
5.2 Main Findings and Practical Implications 74
5.3 Overall Conclusions 76
5.4 References 78
6.0 APPENDICES 80
6.1 Appendix 1: 81
6.2 Appendix 2: 82
6.3 Appendix 3: 82
6.4 Appendix 4: 83
6.5 Appendix 5: 83
6.6 Appendix 6: 84
6.7 Appendix 7: 84

6.8 Appendix 8: 85
6.9 Appendix 9: 85
6.10 Appendix 10: 86
6.11 Appendix 11: 87
6.12 Appendix 12: 87
6.13 Appendix 13: 88
6.14 Appendix 14: 88
6.15 Appendix 15: 89
6.16 Appendix 16: 89
6.17 Appendix 17: 90

LIST OF TABLES

Table 2-1. Monthly precipitation (mm) at the study site for 1996, and long-term averages for nearby weather stations from 1945-82 and 1966-90......... 12

Table 2-2. Mean monthly maximum and minimum temperatures (°C) for 1996, and the long-term average from 1945-82.............................. 12

Table 2-3. Description of treatments based on the unweighted mean proportion of stem, leaf and total dry matter removed from individual alfalfa plants at time of application (SE=standard error, N=sample size)........................ 14

Table 2-4. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean days of post-treatment regrowth required to reach a harvestable alfalfa stand (SE=standard error, N=sample size)... 17

Table 2-5. Effect of defoliation technique, height of defoliation and corresponding interaction on least squares mean herbaceous regrowth of post-treatment alfalfa (SE=standard error, N=sample size)........................ 18

Table 2-6. Effect of defoliation technique, height of defoliation and corresponding interaction on least squares mean total pre and post-treatment production of alfalfa (SE=standard error, N=sample size)................ 18

Table 2-7. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean density of primary and secondary stems of post-treatment alfalfa (SE=standard error, N=sample size)... 19

Table 2-8. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean height of secondary stem origin of post-treatment alfalfa (SE=standard error, N=sample size).. 20

Table 2-9. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean crude protein (CP) and neutral detergent fiber (NDF) content of post-treatment alfalfa (SE=standard error, N=sample size).. 20

Table 3-1. Monthly precipitation (mm) at study site for 1997 and long-term averages for nearby weather stations from 1945-82 and 1966-90......... 33

Table 3-2. Mean monthly maximum and minimum temperatures (°C) for 1997 and the long-term average from 1945-82.................................... 34

Table 3-3. Description of the four treatments employed in 1997 (AUE was defined as an animal unit equivalent whereby one AUE equalled one-454kg nonlactating beef cow or the equivalent in wapiti liveweight; AUM was defined as the potential forage intake of one AUE for a period of one month).. 34

Table 3-4. Effect of sward management system and sampling date on least squares mean soluble protein content of alfalfa taproots (SE=standard error, N=sample size).. 43

Table 3-5 Least squares mean soluble protein and total nonstructural carbohydrate levels in alfalfa taproots sampled October 10, 1997, under four treatments.. 44

Table 3-6. Least squares mean white bud density adjusted for crown area, crown depth and taproot diameter in alfalfa sampled April 21 and October 10, 1997, prior to and following four SMS treatments. Standard error of means are presented in parentheses.. 44

Table 4-1. Description of 1997 grazing trials.. 57

Table 4-2. Predicted DMI (dry matter intake rate in grams dry matter/minute) at maximum available biomass observed in grass-dominated (2630 kg/ha) and alfalfa-only (2840 kg/ha) stands based on significant regression equations from this and previous studies.. 69

LIST OF FIGURES

Figure 2-1. Total daily precipitation (mm) at the experimental site during the 1996 growing season.. 11

Figure 3-1. Total daily precipitation (mm) at the experimental site during the 1997 growing season.. 33

Figure 3-2. Field diagram of experimental design.. 35

Figure 3-3. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the GZHY treatment (grazed 6/5 to 6/19, hayed 7/31) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.................................. 39

Figure 3-4. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the HYGZ treatment (hayed 7/2, grazed 7/31 to 8/16) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.................................. 40

Figure 3-5. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the GZGZ treatment (grazed 6/5 to 7/31, grazed 8/16 to 8/31) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis........................ 41

Figure 3-6. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the HYHY treatment (hayed 7/2, hayed 8/16) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.. 42

Figure 4-1. Estimated dry matter intake rate (g/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=3.15E\text{-}09X^3-1.04E\text{-}05X^2+0.0125X-0.34$, $R^2=.81$) and grass-dominated (dashed line, $Y=31.7X/(1769.8+X)$, $R^2=.41$) stands.......... 61

Figure 4-2. Estimated bite size (g dry matter/bite) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=1.73E\text{-}10X^3-5.57E\text{-}07X^2+5.88E\text{-}04X-0.09$, $R^2=.88$) and grass-dominated (dashed line, $Y=145.1X/(553780+X)$, $R^2=.56$) stands........ 62

Figure 4-3. Phases of bite selection behavior by foraging wapiti in relation to estimated bite size (g dry matter/bite) and total available herbaceous biomass (kg/ha) in alfalfa-only stands.. 63

Figure 4-4. Bite rate (bites/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=55e^{(-0.5[\ln(X/762.6)/0.95]^\wedge 2)}$, $R^2=.87$) and grass-dominated (dashed line, $Y=-1.282E-05X^2+0.033X+22.4$, $R^2=.27$) stands........................... 65

Figure 4-5. Estimated crude protein intake rate (grams/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=8.71E-10X^3-2.94E-06X^2+3.71E-03X-0.42$, $R^2=.96$) and grass-dominated (dashed line, $Y=4.39X/(2363+X)$, $R^2=.34$) stands............... 66

Figure 4-6. Estimated digestible energy intake rate (kcal/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=1.01E-08X^3-3.45E-05X^2+0.043X-3.47$, $R^2=.95$) and grass-dominated (dashed line, $Y=78.1X/(1825+X)$, $R^2=.39$) stands....... 67

Figure 5-1. Relationships of estimated wapiti dry matter intake (grams/minute) and available herbaceous biomass (kg/ha) as described in this and other studies.. 77

1.0 INTRODUCTION

1.1 Historical Background

The origins of wildlife farming can be traced throughout history and the world (Teer et al. 1993). Husbandry of wildlife dates back to ancient times and has not been restricted to early domestication of conventional domestic livestock (Hudson 1989). Deer have been farmed for antlers and venison since ancient times (Hudson 1989).

Game farming, the intensive husbandry of wild stock in penned conditions, has grown tremendously in New Zealand and North America since 1970 (Teer et al., 1993). As of 1990, the cervid farming industry in New Zealand had more than one million animals, mostly red deer (*Cervus elaphus*) on more than 5000 farms (Drew 1991), while Teer et al. (1993) report 130,000 bison (*Bison bison*) and 55,813 deer of various species on commercial game farms in the United States of America (USA) as of 1992. Teer et al. (1993) also report 57,365 commercially farmed cervids in Canada including reindeer (*Rangifer tarandus*), fallow deer (*Dama dama*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), wapiti (*Cervus elaphus*), wapiti-red deer crosses, and red deer. By 2000, estimated numbers of farmed cervids in Canada reached 118,491 on 1,930 licensed game farms and are further categorized by species head count as 57% wapiti, 13% wapiti-red deer crosses or red deer, 15% fallow deer and 15% white-tail deer (Nixdorf 2001). In Alberta, 597 cervid farms held a total of 32,316 wapiti, 7,731 white-tail deer, and 500 individuals of other cervid species as of April, 2001 (Huedepohl, C., personal communication, April 23, 2001[*]). These numbers demonstrate the dominance of wapiti as the most commonly farmed cervid in Alberta and Canada.

1.2 Industry Overview and Research Rationale

Renecker (1988) and Hudson and Adamczewski (1990) described many practical aspects of wapiti farming in Canada. They report a distinct trend towards intensive production of deer on farms employing higher than natural stocking densities to maximize profitability, especially with the high costs of capital infrastructure (mostly fencing costs) relative to more conventional livestock operations. In Alberta, which has the largest numbers of farmed wapiti in Canada (Nixdorf 2001), the trend towards intensive management has been indirectly reinforced by stringent government regulations dictating the licensing and designation of lands used for cervid farming, a government administered animal inventory system, and laws requiring tall and expensive paige-wire fences on cervid farms (Province of Alberta 1994). As a result, most Albertan and other Canadian wapiti farms have been developed on lands once used for beef cattle pasture or cultivated cropland (Renecker 1988), which, in general, are more productive than marginal lands. A survey of Alberta cervid farms (n=50) showed a distinct reliance on tame pasture with a mean ratio of tame to native acreage of 1.86 to 1 +/- 0.08 as expressed in a 95% confidence interval (unpublished data, Arthur,R.L. 1993, see Appendix 1).

---

[*] Livestock Diversification Officer, Diversified Livestock Branch, Animal Industry Division, Alberta Agriculture and Rural Development

Most tame pasture management recommendations for Canadian wapiti farms are derived from prior pastoral research and experience with conventional livestock. Typically, supplemental winter feeding programs on western Canadian wapiti farms begin in early November and end with spring green-up in mid to late April (Renecker 1988). Pastures are a primary source of food during the growing season with alfalfa (*Medicago sativa* L.) and other legumes used as major components of tame pasture stands (Thorleifson 2001). Research studies of wapiti on tame pastures in North America are limited and largely restricted to feeding trials at various points in time where dietary preferences of farmed wapiti were estimated from foraging bouts on patchwork pastures comprised of many grasses and legumes (Fargey 1987; Berg and Gillund 1992). Results from these studies vary with season/stage of forage growth, but generally imply that legumes, including alfalfa, are preferred high quality summer foods for farmed wapiti relative to grasses. This notion concurs with studies of red deer on tame pastures in New Zealand (Hunt and Hay 1992).

Alfalfa is recognized as a dominant forage for wapiti on pasture or on winter supplemental feeding programs (Klein 1997; Thorleifson 2001). The choice of alfalfa as the main pasture legume for farm-raised wapiti in western Canada stems largely from the plant's status as the oldest cultivated forage crop in the world and a mainstay in the production of livestock products (Hanson 1988). It is recognized as a superior pasture legume for many classes of livestock because of high yield, excellent forage quality, fair persistence under grazing and wide climatic and soil adaptation (Van Keuren and Matches 1988). In Canadian prairie provinces, alfalfa is a preferred hay crop, the most-used legume for tame pasture and the standard recommended legume species in forage seeding guides published by government agricultural extension agencies (Alberta Agriculture 1983; Saskatchewan Agriculture and Food 1997). It is commonly grown in mixtures with cool season grasses, including various wheatgrasses and bromegrasses, across western Canada for beef cattle and sheep (Van Keuren and Matches 1988). This also applies on western Canadian wapiti farms (Klein 1997; Thorleifson 2001).

Canadian wapiti farmers commonly employ 50 to 80% (and up to 100%) alfalfa in pasture stands because of the high quality of forage produced and the minimal risk for bloat relative to conventional livestock (Haigh and Hudson 1993; Klein 1997). Articles in industry magazines and government extension publications furnish wapiti farmers with general recommendations for managing alfalfa stands or inclusion of alfalfa in forage mixtures (Klein 1997; Anderson et al. 2000; Thorleifson 1998, 2001). However, research and industry have failed to advance beyond the general observance that alfalfa and other legumes may be preferentially eliminated from wapiti pastures by repeated grazing under continuous grazing systems (Berg and Gillund 1992).

Specific study of individual plant responses of alfalfa and other tame forages to grazing by farmed wapiti is lacking. This void reflects a traditional approach to alfalfa pastoral research following the concept that alfalfa subjected to grazing does not differ appreciably in defoliation management from that harvested for hay (Van Keuren and Matches 1988). Hence, most cultivars are neither developed nor evaluated under grazing (Brummer and Moore 2000). However, cursory observation by professional livestock managers indicates defoliation patterns on tame pastures grazed by wapiti differ distinctly from those grazed by cattle or bison (Klein 1997; Van Lent-Staden, J., personal communication, April 20, 1995[*]), yet controlled comparisons of the effects of those defoliation differences on individual plants are simply not available. This is indicative of a distinct industry need for more research of the plant-animal interface to improve pasture management strategies for wapiti farmers.

1.3 Wapiti Feeding Strategies

Differential defoliation patterns by wapiti on pasture relative to other large ruminants leads to the notion that variation in feeding strategies and grazing prehensile mechanics among herbivores may have corresponding effects on pasture health and regrowth potential. Hence, a short review of the ecophysiological nature of wapiti relative to other ruminants is of value in establishing a baseline perspective of the plant-animal interface of interest in this study.

Hoffman (1989) and Langer (1988) submit ruminant evolution has proceeded in a "bush-like" or multidirectional progression (as opposed to a "ladder-like" or unidirectional progression) from ancestry to present day. The main determinant of evolution has been climatic change, with resultant shifts in vegetation producing a wide and dynamic variety of habitats in open and forested biomes (Langer 1988; Wing 1998; Janis et al. 2000). Attempts to classify feeding niches of ruminants have focused largely on three properties of vegetation: food quality, quantity and botanical composition (Gordon and Illius 1996). From this basis, two general theories categorizing ruminants into feeding types have emerged, both are well documented but are not mutually exclusive. The first has been described as a diet quality assumption by Gordon and Illius (1996). It was originally theorized by Bell (1970, 1971) and Jarman (1974) who distinguished feeding categories of antelope based on feeding style and diet. Geist (1974) labeled it the Jarman-Bell principle, then further refined it with the statement that a negative relationship between diet quality and body mass was fundamental to the principle as a determinant of food selectivity. The second has been termed a diet type assumption by Gordon and Illius (1996) and primarily advances the views of Hoffman (1973, 1989) who stated forage quality and availability within a biome drives evolution of ruminant anatomy to achieve the required function to facilitate effective digestion. Hoffman classified three main ruminant feeding types representing broadly overlapping branches of ruminant evolutionary progression. The three branches represent variations in prehensile and digestive anatomy that determine adaptive ability to consume bulk/roughage grazer diets (mostly grasses), concentrate diets (mostly browse or forbs) or intermediary/mixed diets, and which minimize the importance of body mass as a consistently negative correlate with diet quality. Accordingly, Hoffman categorized wapiti as intermediate feeders, as have numerous other species-comparative studies of digestive anatomy and function (Kay 1987a, 1987b; Baker and Hobbs 1987; Renecker and Hudson 1990; Spalinger et al.

---

[*] Beef Specialist, Animal Industry Division, Alberta Agriculture Food and Rural Development

1993), and studies of diet and feeding patterns (Gates and Hudson 1981, 1983; Hudson and Watkins 1986; Nelson and Leege 1982). On native rangelands in Alberta, wapiti prefer to forage on grassy uplands and openings interspersed with aspen boreal forest where they function predominantly as grazers with diets dominated by graminoids in times of food abundance, but with increased use of available browse in times of food scarcity (Nelson and Leege 1982; Gates and Hudson 1981, 1983; Hobbs et al. 1983; Hudson and Nietfeld 1985). These practical observations are consistent with comparative studies (Gordon and Illius 1988; Janis and Ehrhardt 1988) claiming the prehensile anatomy of a mixed feeder is more akin to a concentrate selector than a grazer. Such anatomical structure would allow the mixed feeder to act as a selective grazer during high resource availability in spring/wet seasons in temperate regions while providing the adaptive option/flexibility to browse efficiently when food abundance declines in winter/dry seasons. Thus, in the wild, a part of the adaptive solution insuring wapiti survival during the critical winter/dry season is a mouth morphology akin to a concentrate selector. This, in effect, means a narrower and more pointed incisor arcade (Gordon and Illius 1988; Janis and Ehrhardt 1988) akin to concentrate selectors like white-tail deer (*Odocoileus virginianus*) or mule deer (*Odocoileus hemionus*) than in grazers like cattle (*Bos taurus*) or bison (*Bison bison*).

In summary, wapiti possess a prehensive arsenal capable of greater feeding selectivity than the dominant herbivore in western Canada upon which tame pasture management recommendations are generally made, namely, cattle. This presents an interesting dilemma to ranchers managing pastures for cervids instead of conventional livestock. Furthermore, the impact of highly selective wapiti on plants may be further intensified under the typically greater stocking rates employed on intensive farming operations than in the wild. Hence, pasture management decisions may differ significantly on cervid farms than on conventional livestock farms. This was a fundamental premise for research in the present study.

1.4 Research Objectives

The general goal of the present work was to study response of alfalfa to use by wapiti with a focus on the plant-animal interface, and with the underlying overall objective of improving pasture management strategies for wapiti farmers. The study was comprised of three separate experiments, addressing the following objectives:

1. To determine the effect of defoliation method and height on origin, regrowth and yield of post-treatment above-ground biomass in alfalfa.
2. To determine the effect of four sward management systems comprised of various combinations of haying and wapiti grazing on root chemistry and regrowth characters in alfalfa during a growing season.
3. To determine the effect of available plant biomass and alfalfa content in tame pastures on estimated dry matter and nutritional intake by wapiti.

The objective of the first experiment was to provide a broad link of simulated wapiti grazing to traditional alfalfa defoliation research. Alfalfa plants at a mid-vegetative stage of growth were defoliated using one of two methods applied to one of three defoliation heights and subsequent post-treatment characteristics studied. The first defoliation method was a conventional "mowing" method which simulated hay defoliation and the second method was a "leaf stripping" method which simulated wapiti grazing. The latter method employed a hand leaf stripping method which produced a post-defoliation stand containing stemmy material devoid of leaves and apical meristems at heights above the normal defoliation height for corresponding conventional mowed treatments. This simulation attempted to produce a defoliation pattern akin to that previously described where post-use alfalfa pastures contain mostly residual stemmy material following selective removal of the more succulent leaves and top growth by wapiti.

The second experiment employed four separate management systems at a field scale level typical of Alberta wapiti farms with the objective of assessing combined effects of haying and wapiti grazing on above-ground biomass and other plant characters including root attributes. Plant-focused studies of alfalfa-wapiti interactions in field scale management systems commonly employed in industry were a major justification for the overall study.

The third experiment in this study was designed to test/validate/expand on studies of nutritional intake and feeding behavior of wapiti done previously on mostly native pastures (Hudson and Nietfeld 1985; Hudson and Watkins 1986; Renecker and Hudson 1990). Animal adaptivity to intake and digesta passage rate constraints may be largely influenced via climatic and environmental effects on food quality and quantity in the wild, but maximizing food and nutritional intake on tame pastures during the growing season is of prime interest to managers of wapiti farms on private lands. Insights into how wapiti respond to pastures with varying alfalfa content and available biomass could be used to develop pastoral management strategies that allow for an optimal foraging response for farmed wapiti on pasture.

In summary, the collective focus in this study was the interaction of wapiti with alfalfa on tame pasture. Three experiments were designed to vary the perspective on this herbivore-plant interaction. The first experiment provided a comparative assessment of the effect of differential defoliation of alfalfa by simulated wapiti grazing and mowing on the subsequent stand produced. The second experiment assessed alfalfa response to sward management systems which employed wapiti grazing and/or haying under field scale pasture conditions. The third experiment was a field scale validation of bioenergetic constraints controlling wapiti intake on tame pastures containing variable alfalfa content. Individual chapters of this work were based on each of the aforementioned experiments and presented in that order. A final synthesis chapter presented general discussion and conclusions derived across all three experiments.

1.5 References

Alberta Agriculture. 1983. Alberta forage manual. Print Media Branch, Alberta Agriculture. Agdex 120/20-4. 87 pp.

Anderson, B., J.T. Nichols and J.C. Henning. 2000. Maintaining and renovating alfalfa pasture stands. p. 64-65. In: North American Elk June/July 2000. Vol. 11, No. 3. North American Elk Breeders Association. Platte City, Missouri.

Baker, D.L. and N.T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Can. J. Zool. 65:1978-1984.

Bell, R.H.V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. p. 111-123. In: Watson, A. (ed.). Animal Populations in Relation to their Food Resources. Tenth Symposium of the British Ecological Society. Blackwell Scientific Publications.

Bell, R.H.V. 1971. A grazing ecosystem in the Serengeti. Scientific American 224:86-93.

Berg, B. and G.M. Gillund. 1992. Seasonal suitability of tame forage varieties for elk. Farming for the future on-farm demonstration program project 87-F007-4 final report. Alberta Agriculture, Food and Rural Development. 15pp.

Brummer, E.C. and K.J. Moore. 2000. Persistence of perennial cool-season grass and legume cultivars under continuous grazing by beef cattle. Agronomy Journal 92:466-471.

Drew, K.R. 1991. Deer farming in New Zealand. p. 113-117. In: Renecker, L.A. and R.J. Hudson (eds.). Wildlife Production: Conservation and Sustainable Development. AFES misc. publ. 91-6. Univ. Alaska Fairbanks, Fairbanks. 601 pp.

Fargey, P.J. 1987. Wapiti selection of grass and legumes. p. 24-26. In: Renecker, L.A. (ed.). Focus on a new industry. Proceedings of the Alberta Game Growers Association Conference 1. Red Deer, Alberta. 110pp.

Gates, C.C. and R.J. Hudson. 1981. Habitat selection by wapiti in a boreal forest enclosure. Naturaliste Can. (Rev. Ecol. Syst.) 108:153-166.

Gates, C.C. and R.J. Hudson. 1983. Forage behaviour of wapiti in a boreal forest enclosure. Naturaliste Can. (Rev. Ecol. Syst.) 110:197-206.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. American Zoologist 14:205-220.

Gordon, I.J. and A.W. Illius. 1988. Incisor arcade structure and diet selection in ruminants. Functional Ecology 2:15-22.

Gordon, I.J. and A.W. Illius. 1996. The nutritional ecology of African ruminants: a reinterpretation. J. Anim. Ecology 65:18-28.

Haigh, J.C. and R.J. Hudson. 1993. Farming wapiti and red deer. Mosby Year-Book, Inc. St. Louis, Missouri. 369 pp.

Hanson, A.A. 1988. Preface. p. xvii-xviii. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Hobbs, N.T., D.L. Baker and R.B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. J. Wildl. Manage. 47:1-16.

Hoffman, R.R. 1973. The ruminant stomach: stomach structure and feeding habits of East African game ruminants. East African Monographs in Biology. Vol. 2. Nairobi: East African Literature Bureau, Box 30022. pp 1-354.

Hoffman, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

Hudson, R.J. 1989. History and technology. p. 11-27 In: Hudson, R.J., K.R. Drew and L.M. Baskin (eds.). Wildlife production systems: Economic utilization of wild ungulates. Cambridge Univ. Press, Cambridge.

Hudson, R.J. and M.T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. J. Range Manage. 38:80-82.

Hudson, R.J. and J.Z. Adamczewski. 1990. Effect of supplementing summer ranges on lactation and growth of wapiti (*Cervus elaphus*). Can. J. Anim. Sci. 70:551-560.

Hudson, R.J. and W.G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. Can. J. Zool. 64:1705-08.

Hunt, W.F. and R.J.M. Hay. 1992. Seasonal differences in pasture species preferences by red and fallow deer in New Zealand. p. 463. In: Brown, R.D. (ed.). The biology of deer. Proceedings of the international symposium on the biology of deer. Mississippi State University. Springer-Verlag New York, Inc. 596 pp.

Janis, C.M. and D. Ehrhardt. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zool. J. Linnean Society 92:267-284.

Janis, C.M., J. Damuth and J.M. Theodor. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone?. Proc. Nat. Academy of Sciences 97(14):7899-904.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. Behavior 48:215-266.

Kay, R.N.B. 1987a. Comparative studies of food propulsion in ruminants, p. 155-170. In: Ooms, L.A., A.D. Degryse and A.S.J.P.A.M. van Miert (eds.). Physiological and pharmacological aspects of the reticulo-rumen. Martinus Nijhoff Publishers. Boston.

Kay, R.N.B. 1987b. Weights of salivary glands in ruminant animals. J. Zool. Lond. 211:431-436.

Klein, L. 1997. Pasture and forages for wapiti. Grazing and Pasture Technology Program Publ. GPP0397. Extension Branch, Saskatchewan Agriculture and Food. 12 pp.

Langer, P. 1988. Anatomical and nutritional adaptations in wild herbivores. p. 185-203. In: The mammalian herbivore stomach: comparative anatomy, function and evolution. G. Fischer. Stuttgart. .

Nelson, J.R. and T.A. Leege. 1982. Nutritional requirements and food habits. p. 323-368. In: Thomas, J.W. and D.E. Toweill (eds.). Elk of North America Ecology and Management. Wildl. Manage. Institute. Stackpole Books. Harrisburg, Pa.

Nixdorf, R. 2001. Specialized livestock inventory and prices update May 10, 2001 [monograph online]. Available from: Rnixdorf@agr.gov.sk.ca . Sustainable Production Branch, Saskatchewan Agriculture and Food. Accessed 2001 May 19.

Province of Alberta. 1994. Livestock Industry Diversification Act and Pursuant Regulations. In: Statutes of Alberta, 1990, Chapter L-22.7 with amendments in force as of January 1, 1992. Consolidated November 17, 1994. Queen's Printer, Edmonton, Alberta.

Renecker, L.A. 1988. Wapiti farming in Canada. p. 118-140. In: Valdez, R. (ed.). Proceedings: First International Wildlife Ranching Symposium. Las Cruces, New Mexico. New Mexico State University. 321 pp.

Renecker, L.A. and R.J. Hudson. 1990. Digestive kinetics of moose (*Alces alces*), wapiti (*Cervus elaphus*), and cattle. Anim. Prod. 50:51-61.

Saskatchewan Agriculture and Food. 1997. Saskatchewan forage crop production guide.

Spalinger, D.E., C.T. Robbins and T.A. Hanley. 1993. Adaptive rumen function in elk (*Cerphus elaphus nelsoni*) and mule deer (*Odocoileus hemionus hemionus*). Can. J. Zool. 71:601-610.

Teer, J.G., L.A. Renecker and R.J. Hudson. 1993. Overview of wildlife farming and ranching in North America. Trans. N. Am. Wildl. Nat. Resour. Conf. 58:448-459.

Thorleifson, I. 1998. Pasture mixes and management for elk. p. 32-33. In: The Canadian Elk and Deer Farmer Spring 1998. Vol. 5(2). Calgary, Alberta, Canada.

Thorleifson, I. 2001. Pasture mixes and management for elk. p. 77. In: The Canadian Elk and Deer Farmer Early Spring 2001. Vol. 8(2). Calgary, Alberta, Canada.

Van Keuren, R.W. and A.G. Matches. 1988. Pasture production and utilization. p. 515-538. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Wing, S.L. 1998. p. 37-60. In: Janis, C.M., K.M. Scott and L.L. Jacobs (eds.). Evolution of tertiary mammals of North America. Cambridge Univ. Press. Cambridge, U.K.

2.0 REGROWTH IN VARIABLY DEFOLIATED ALFALFA

2.1 Introduction

There is generally widespread acceptance that alfalfa response (*Medicago sativa* L.) to defoliation by grazing does not differ appreciably from alfalfa harvested for hay (Van Keuren and Matches 1988). As a result, most pasture management recommendations for alfalfa have been derived from defoliation management research focusing on stage of growth at defoliation, defoliation height and defoliation frequency as major determinants of plant health and stand longevity (Sheaffer et al. 1988). Most grazing-tolerant alfalfa cultivars in North America have been selected for broad crowns or creeping rootedness (ie. the ability to initiate new shoots from lateral roots) (Heinrichs 1963, 1978); and more recently, for persistence under continuous stocking by cattle, prolific fall budding, decumbent growth habit, stubble leaf area retention, early fall dormancy, deep-set crown development and the ability to maintain root carbohydrate levels under grazing (Smith et al. 1989, 1992; Wolf and Allen 1990; Bouton et al. 1991; Smith and Bouton 1993). These approaches to plant selection assume minimal variation in foraging strategies and grazing mechanics among livestock species utilizing tame pasture. Various studies report differences in the effects of grazing versus mowing or haying on alfalfa (Leach 1979; Counce et al. 1984; Allen 1985), and research into grazing systems indicates persistence of alfalfa is generally greater under some form of rotational grazing than under continuous grazing (Smith et al. 1989, 1992; Smith and Bouton 1993; Brummer and Bouton 1991, 1992). However, few works have considered variation in bite dimensions and prehensile mechanics among livestock species as a factor of consequence in selecting or managing plants for grazing tolerance.

Numerous studies report distinct variability in bite dimensions and prehensile techniques of large ruminant herbivores (Willms 1978; Hudson and Nietfeld 1985; Gordon and Illius 1988; Janis and Ehrhardt 1988; Hoffman 1989). Grazers (eg. cattle, bison) have a relatively flat, wide, non-protruding incisor arcade favoring non-selective, high volume intake of spatially bunched foods that are typically found on more open habitats. Conversely, mixed and concentrate feeders (eg. wapiti, white-tail deer) have more curved, narrow, protruding incisor arcades which allow selective prehension of highly digestible foods. Cattle are known to exhibit a larger incisor arcade breadth than wapiti (Gordon and Illius 1988), and are capable of higher forage intake rates via larger bite sizes (Hudson and Nietfeld 1985). Laca et al. (1992) compared cattle grazing homogeneous stands of alfalfa, versus grass, and found bite size/volume was largely a function of bite area and bite depth into the sward from the top downwards, as well as sward bulk density. For cattle, bite area and depth into the sward correlate positively with sward height and negatively with sward bulk density. Laca et al. (1992) also report that in taller, less dense stands, individual bites by cattle in a foraging time frame are initially smaller due to spatially separate portions of plant individuals, and cattle subsequently compensate by increasing bite depth into the sward and maximize bite volume by increasing tongue extension into the sward. Jiang and Hudson (1994) report contrasting results for wapiti grazing heterogeneous grass-dominated swards. They observed wapiti selecting foods vertically within the sward, taking deeper and larger sized bites in spring when stem and leaf components are the most comparable in form and digestibility. However, in summer and fall, they report wapiti are able to graze less deep in the sward yet still maximize diet quality by selectively prehending preferred plants and/or plant parts. For wapiti, vertical selection is largely a balancing act between bite size and diet quality.

In summary, cattle use their tongues to sweep and prehend forage on a horizontal plane primarily along the top of the forage stand (Laca et al. 1992), while wapiti use their lips, dental pad and lower incisors to grasp, break and ingest individual plant parts along a repetitive vertical plane within the stand (Willms 1978; Jiang and Hudson 1994). The analogy of a "lawn-mower" (whether by mowing or grazing by cattle) versus a "leaf-stripper" (wapiti) may apply and is of interest where graziers manage wapiti on pasture. These differences imply alfalfa cultivars selected for thinner primary stems, which are prone to removal by wapiti, or cultivars which exhibit rapid regrowth from secondary stems following defoliation, may foster increased efficiency of use by wapiti.

The recorded differences in mowing and the prehensile techniques of wapiti, relative to other ruminants like cattle, provided the basis for the first experiment in the present study. The objective of this experiment was to determine the effect and interactions of defoliation method and height on origin, timing, yield and quality of post-treatment above-ground biomass in alfalfa. Of specific interest were the comparative effects of mowing versus "stripping" which simulated defoliation by wapiti on alfalfa, and interactions with height of defoliation. I hypothesized that defoliation by stripping would result in greater secondary (axillary-derived) stem density, quicker recovery following defoliation, similar or greater forage yields, and reduced forage quality (due to stem retention) than in mowed stands.

2.2 Materials and Methods

2.2.1 Experimental Area

The experiment was conducted at 53° 03' 30" North, 110° 51' 30" West near Vermilion, in east central Alberta, Canada. The site contained loam textured Orthic Black Chernozemic soils on a morainal parent material with level to gently undulating surface expression (Agriculture Canada 1988). It was situated in the aspen parkland ecoregion of Alberta which has been described climatically and ecologically as a transition zone between boreal forest and grassland environments (Strong and Leggat 1992). This ecoregion is characterized by a cool, continental climate with short, warm summers and long, cold winters (Wonders 1969). Total mean annual precipitation for the ecoregion is 412mm with a median summer precipitation of 259mm where the majority of precipitation falls in June and July. (Strong and Leggat 1992). Prior to this research, the site was cultivated for about 60 years and was part of a mixed farming operation alternating between cereal cropping and mixed tame pasture.

The site was established in April 1996 on a mature stand of alfalfa (*Medicago sativa* L. cv. Alfagraze) seeded in May 1992 at 9kg/ha (inoculated with *Rhizobium meliloti*) at a 15cm row spacing and subsequently cut for hay once annually to a height of 10cm between July 1-15 from 1993 to 1996 inclusive. Fertilizer was applied in a one-time deep banding operation prior to seeding in May 1992 at a rate of 30kg N ha^{-1}, 150kg P ha^{-1}, 30kg S ha^{-1}, and 30kg K ha^{-1}. Sethoxydim and 2,4-DB were applied to the site during the 1995 growing season at rates of 556 and 1698g ha^{-1} a.i., respectively, to eliminate grasses and non-leguminous weeds. Prior to initiating the experiment in 1996, plant species other than alfalfa were present in the stand at a combined total of <1% of above-ground biomass. This included dandelion (*Taraxacum officinale* Weber), yarrow (*Achillea millefolium* L.), aster (*Aster spp.*), northern bedstraw (*Galium boreale* L.) and foxtail barley (*Hordeum jubatum* L.). Stand composition was determined from four randomly selected 20 x 100cm clip plots of above-ground live herbaceous biomass taken in each replicate area on the entire experimental site in late May, 1996, segregated by species, dried at 60°C for 48 hrs and weighed.

2.2.2 Climatological Data

Precipitation at the site was measured daily throughout 1996 using a cylindrical rain gauge graduated to 1mm. Precipitation events showing the distribution of rainfall during the growing season are depicted in Figure 2-1. Daily rainfall totals were pooled to determine total monthly precipitation for the experimental site as presented in Table 2-1. Long-term average monthly precipitation for two nearby Environment Canada weather stations (at Vermilion, about 30km north of the site, data from 1945-82; and at Fabyan North, about 11km southwest of the site, data from 1966-90) are also presented in Table 2-1 (Environment Canada 1993; Environment Canada 1999).

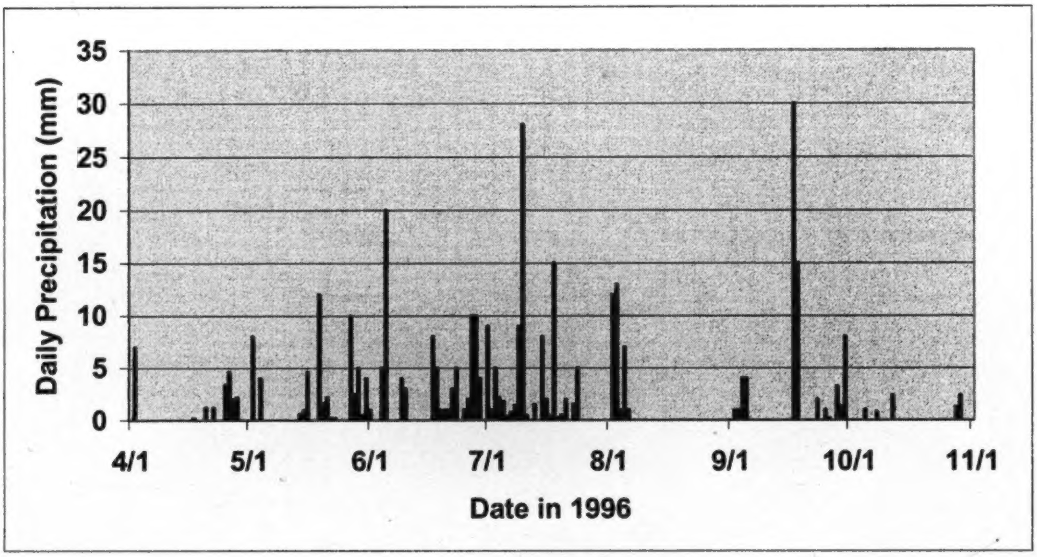


Figure 2-1. Total daily precipitation (mm) at the experimental site during the 1996 growing season.

Table 2-1. Monthly precipitation (mm) at the study site for 1996, and long-term averages for nearby weather stations from 1945-82 and 1966-90.

Month	Study Site 1996	Vermilion 1945-82	Fabyan 1966-90
January	15.8	19.8	21.6
February	9.8	12.9	13.5
March	17.2	17.9	21.9
April	24.8	19.7	21.0
May	73.1	40.0	38.6
June	96.4	75.9	78.2
July	111.8	78.5	79.6
August	29.8	62.8	58.6
September	70.9	35.6	38.2
October	7.8	15.7	16.2
November	5.0	14.7	16.0
December	40.0	20.2	23.0
Total	502.4	413.7	426.5

Daily maximum and minimum temperatures were recorded at the experimental site during the growing season of 1996 and at the Environment Canada weather station at Fabyan North (Environment Canada 1999). These data were used to compute mean monthly maximum and minimum temperatures for the experiment site in 1996 which are presented in Table 2-2 with long-term averages for the Environment Canada weather station at Vermilion (Environment Canada 1993). A killing frost of -5°C occurred at the site on October 16, 1996.

Table 2-2. Mean monthly maximum and minimum temperatures (°C) for 1996, and the long-term average from 1945-82.

Month	Max.1996	Min. 1996	Max. 1945-82	Min. 1945-82
January	-15.8	-27.5	-12.9	-23.7
February	-6.2	-19.8	-7.6	-19.1
March	-4.2	-16.3	-2.1	-13.6
April	9.5	-2.6	9.2	-3
May	12.3	2.1	17.6	3.4
June	19.4	8.0	21.1	8.0
July	22.1	10.2	23.0	10.0
August	24.6	9.1	22.5	8.7
September	15.2	3.9	16.5	3.3
October	9.2	-3.3	10.8	-2.0
November	-8.8	-17.1	-1.0	-11.0
December	-13.0	-23.1	-9.6	-19.7

2.2.3 Experimental Design

The experiment used a randomized complete block design with 6 replicate blocks each containing a 3x2 factorial arrangement of treatments. Each replicate contained 6-2 x 2m plots to which treatments were randomly allocated. Main factors were defoliation height (2.5, 7.5, and 15 cm) and defoliation technique (mowing, stripping). Defoliation heights used in this experiment were based on commonly researched defoliation heights described by Sheaffer et al. (1988). The mowing technique was designed to simulate hay cutting or grazing by cattle, while the stripping technique was designed to simulate wapiti grazing.

Defoliation treatments were applied when the majority of alfalfa plants within a block were at the mid-vegetative stage of growth, as described by Fick et al. (1988), had achieved a mean height of 25cm, and at least 90% of ground area was covered with herbaceous biomass. These criteria were collectively called trigger criteria. As a result, defoliation treatments were applied to blocks 1 and 2 on June 4, and remaining blocks on June 6. Mean stand height at treatment application was uniform, 25 ± 3cm (mean ± sd). The choice to apply treatments at a specific stage of growth was based on the well documented premise that harvest by phenology is superior to harvest by fixed dates in insuring consistent forage yield and quality (Sheaffer et al. 1988). Furthermore, treatment application dates for this experiment coincided with the wapiti calving season, a period when high quality forage supplies are critical to wapiti productive success and, as such, a time when effective pasture management is particularly critical (Haigh and Hudson 1993).

2.2.4 Pre-Treatment Monitoring

Assessment for the stage of growth trigger criteria was performed daily prior to treatment application using a randomly located one meter line transect at least 0.5m inside the edge of each plot. Along each transect, a vertical point frame was used to employ a first hits method at 10cm intervals as described by Cook and Stubbendieck (1986) to determine phenological stage of growth, mean sward height, and herbaceous cover based on a total of 10 points per one meter transect. For each vertical point sampled, the first part of a plant contacted was designated as a "first hit", following which sward height above-ground level was estimated by measuring the maximal length of the primary stem attached to the part of the plant first hit. Phenological stage of growth of the plant for which the "first hit" occurred was recorded according to Fick et al. (1988) to verify attainment of trigger criteria. Vertical points hitting bare ground were used to determine herbaceous cover.

2.2.5 Treatment Application

When trigger criteria were attained in all plots within a replicate block, defoliation was performed to one of the three specified heights using one of the two specified defoliation techniques on a 1.5 x 1.5m central area of each plot. Mowing was performed using hand-held hedge clippers. Stripping was performed by clamping a person's fingers around each primary stem at the specified defoliation height, then sliding the hand firmly upwards to the top of the plant while still clasping the stem. Mowed and stripped biomass was immediately removed from each plot. Validation of the stripping method by comparison of stripped plants to actual wapiti-grazed plants on the same stand was not possible at the experimental area. Therefore, I relied on ocular estimates by an expert wapiti grazier (Van Lent-Staden, personal communication, June 4, 1996*) and previous studies of bite characteristics of wapiti within a sward (Jiang and Hudson 1993, 1994) to deem the stripping method effectively simulated an alfalfa stand following moderate to heavy grazing by wapiti. Stripping simulated wapiti utilization to the point where food selection had proceeded vertically from the top of the sward downward with removal of approximately 10cm of top growth, followed by selective leaf removal from remaining stem material as a result of vertical selection of leafy plant parts within the sward as described by Jiang and Hudson (1994). Untreated outside portions of each 2 x 2m plot were power mowed to a height of 10cm at treatment application to minimize shading effects within plots.

In addition, prior to treatment application, four to eight plants were randomly selected inside each 1.5 x 1.5m plot area. As treatments were applied to each of these plants, above-ground biomass was separated into two pools, biomass removed at treatment and biomass remaining on plants. Each of these pools was further dissected into stem and leaf fractions, then dried at 60°C for 48 hrs and weighed on a dry matter (DM) basis. This allowed separation of stem and leaf biomass removed from and remaining on plants following mowing and stripping (see Table 2-3). Roots of these plants were also collected intact by digging to a 20cm depth using the method of Brummer and Bouton (1991). Plants were packed in ice, transported to the laboratory where the roots were washed free of soil under cold water, then measured for crown area. Crown area was estimated as the product of two perpendicular measures of crown diameter following removal of vegetative biomass simulating the method of Brummer and Bouton (1991). The sum total of crown area for all plants sampled within each plot was then used as a divisor to adjust

Table 2-3. Description of treatments based on the unweighted mean proportion of stem, leaf and total dry matter removed from individual alfalfa plants at time of application (SE=standard error, N=sample size).

Treatment	Stem Removed (%)	SE	Leaf Removed (%)	SE	Total Removed (%)	SE	N
Mowed to 2.5cm	93.3	0.5	99.7	0.1	96.5	0.2	29
Mowed to 7.5cm	61.2	1.6	77.6	1.6	70.9	1.1	28
Mowed to 15cm	39.1	1.8	62.3	1.4	52.6	1.4	25
Stripped to 2.5cm	6.7	0.4	99.7	0.1	57.1	1.6	27
Stripped to 7.5cm	3.8	0.2	80.5	1.1	46.5	1.3	28
Stripped to 15cm	3.4	0.3	66.5	2.1	36.9	1.5	28

---

* Beef Specialist, Animal Industry Division, Alberta Agriculture Food and Rural Development

the sum total of above-ground biomass removed and remaining at treatment in each plot. This adjusted for variation in the size of individual plants within each plot sampled in a manner similar to that of Brummer and Bouton (1991) and yielded data required to determine post-treatment regrowth and total above-ground biomass production over the duration of the experiment (see 2.2.7 below).

2.2.6 Post-treatment Monitoring

Post-treatment herbaceous biomass was assessed daily in the central 1 x 1m subplot of each treated 1.5 x 1.5m portion of each original 2 x 2m plot. Methods used were the same as those previously described for pre-treatment assessment of plots. When regrowth in each plot proceeded to the point where the mean stand height was at least 25cm and herbaceous cover exceeded 90%, the plot was deemed to contain a harvestable stand approaching peak biomass in a predominantly mid-vegetative state (as previously described) and subsequently subjected to post-treatment harvesting and measurement of dependent variables.

2.2.7 Post-treatment Harvesting

Upon attaining the criteria of a harvestable stand, all above-ground herbaceous biomass was harvested in one randomly selected 20 x 100cm clip plot in each 1 x 1m central treated subplot area harvested perpendicular to seed rows. Clip plot area was similar to that employed by Smith et al. (1992) and Smith and Bouton (1993). Samples were oven dried at 60°C for 48 hrs and weighed, then retained as air dry samples until chemical analyses for forage quality parameters were performed. The number of days between treatment application and harvest of post-treatment biomass was recorded for each plot as a measure of days required to reach a harvestable state.

Four to eight plants were randomly selected from the remaining unclipped portion of each 1 x 1m central treated subplot, and were collected intact by digging to a 20cm depth using the method of Brummer and Bouton (1991). Plants were packed in ice, transported to the laboratory where the roots were washed free of soil under cold water, then measured for crown area. Crown area was estimated as the product of two perpendicular measures of crown diameter following removal of vegetative biomass simulating the method of Brummer and Bouton (1991). Primary and secondary stems were counted for each plant inclusive of all pre and post-treatment stems present. Primary stems were those originating from the root crown zone as defined by Teuber and Brick (1988). Secondary stems were defined as live stems originating from axillary buds on primary stems above the crown zone. For each secondary stem, the height of origin above the upper limit of the root crown zone was measured. Finally, above-ground biomass of whole plants was dissected and segregated into primary and secondary derived portions. Secondary derived biomass was further segregated into 3 height of origin classes (0-2.5cm, 2.51-7.5cm, >7.5cm). Biomass pools were oven dried at 60°C for 48 hrs and weighed. Individual per plant measures of primary and secondary stem biomass and stem counts were divided by crown area to adjust for variability in individual plant size when determining primary and secondary stem densities. Individual per stem measures of height of origin of secondary stems above the crown were not separated by individual plants prior to data analysis as both plants and stems thereon were effectively nested within treatment plots.

The above plant data, when combined with data collected from destructively harvested plants at treatment application, allowed separate estimates of total post-treatment regrowth and total pre and post-treatment herbaceous biomass production for each plot. Regrowth was estimated using means calculated across all plants sampled within each plot where:

> Regrowth biomass = (post-treatment harvested biomass) – (stem and leaf left on at time of treatment application)
>
> and where: units of measure were g DM/cm^2 of crown area.

Similarly, total biomass production per plot was estimated using means calculated across all plants sampled within each plot where:

> Total harvested biomass = (post-treatment harvested biomass) + (stem and leaf removed at time of treatment application)
>
> and where units of measure were g DM/cm^2 of crown area.

2.2.8 Chemical Analyses

Herbaceous biomass samples from post-treatment harvested clip plots were subsampled separately for analysis of crude protein and NDF (neutral detergent fiber) as indicators of forage quality. Crude protein was analyzed using a mixed catalyst Kjeldahl method (AOAC 1990) where subsamples were digested in sulfuric acid in the presence of a copper sulfate/titanium dioxide catalyst to convert organic nitrogen to ammonium sulfate, then ammonia from steam distilling titrated with a standard acid to derive nitrogen content and a 6.25 multiplier applied to estimate crude protein. NDF was analyzed using a neutral detergent fiber-amylase method (Undersander et al. 1993a, 1993b) whereby a neutral detergent solution was used to solubilize proteins and crude oils; EDTA was used to chelate calcium and remove pectins at boiling temperatures; and heat stable amylase used to remove starch.

2.2.9 Statistical Analyses

Analysis of variance procedures in SYSTAT (SPSS Inc. 1999) were used to analyze data. Variation in dependent variable data was partitioned into replicate, height of defoliation and defoliation technique main effects and their corresponding interactions. Main effects and interactions of interest were tested with corresponding replicate interaction terms (see Appendices 2 to 9) according to the method of Hicks (1973). Where analysis of variance identified significant effects, individual degree of freedom orthogonal contrasts were conducted to confirm significance ($p<0.05$) of pairwise differences among means of main effects. Tukey's Studentized range statistic was used for comparison of means of significant ($p<0.05$) interactions.

2.3 Results

2.3.1 Regrowth Period

Following treatment application, the regrowth period required to meet the criteria of a harvestable stand was five days shorter ($p<0.001$) for stripped plants than mowed plants (Table 2-4). For plants defoliated to a 15cm height, the regrowth period was three ($p<0.05$) and ten ($p<0.001$) days shorter than for plants defoliated to7.5 and 2.5cm, respectively. The interaction of defoliation technique and height was not significant ($p>0.05$).

Table 2-4. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean days of post-treatment regrowth required to reach a harvestable alfalfa stand (SE=standard error, N=sample size).

Effect	Comparison	Days of Regrowth	SE	N
Defoliation technique	Mowed	21 a	1	18
	Stripped	16 b	1	18
Defoliation height	2.5cm	23 a	1	12
	7.5cm	20 b	1	12
	15cm	13 c	1	12
Technique x Height	Mowed to 2.5cm	25	1	6
	Mowed to 7.5cm	22	1	6
	Mowed to 15cm	16	1	6
	Stripped to 2.5cm	21	1	6
	Stripped to 7.5cm	17	1	6
	Stripped to 15cm	11	1	6

Within each effect, means in the same column with the same letter are not significantly different ($p<.05$).

Based on above average rainfall from April through July (Table 2-1), soil moisture supplies were likely not limiting relative to normal during treatment applications and the regrowth period. Furthermore, there were more than 20 daily rainfall events during the June 4 to July 4 period (Figure 2-1) with near long-term mean temperatures (Table 2-2). This one-month period coincided with treatment applications beginning June 4 and the subsequent majority of regrowth. Therefore, effects of inadequate soil moisture on regrowth were unlikely or minimal for not more than a few days consecutively in this experiment.

2.3.2 Regrowth and Total Herbaceous Biomass

Herbaceous regrowth following treatment application ($p<0.05$, Table 2-5) and total herbage produced including all pre and post-treatment biomass ($p<0.001$, Table 2-6) were both greater in mowed than stripped alfalfa. Additionally, total herbage production was lower ($p<0.05$) for alfalfa defoliated to a 15cm height than at 7.5 or 2.5cm heights (Table 2-6) and a similar but insignificant trend ($p>0.05$) was apparent for herbaceous regrowth (Table 2-5). The defoliation technique by height interaction did not affect regrowth or total biomass significantly ($p>0.05$).

Table 2-5. Effect of defoliation technique, height of defoliation and corresponding interaction on least squares mean herbaceous regrowth of post-treatment alfalfa (SE=standard error, N=sample size).

Effect	**Comparison**	**Regrowth Biomass (g DM/cm^2 crown area)**	**SE**	**N**
Defoliation technique	Mowed	0.32 a	.06	18
	Stripped	0.16 b	.06	18
Defoliation height	2.5cm	0.26	.07	12
	7.5cm	0.27	.07	12
	15cm	0.18	.07	12
Technique x Height	Mowed to 2.5cm	0.34	.10	6
	Mowed to 7.5cm	0.33	.10	6
	Mowed to 15cm	0.28	.10	6
	Stripped to 2.5cm	0.18	.10	6
	Stripped to 7.5cm	0.22	.10	6
	Stripped to 15cm	0.09	.10	6

Within each effect, means in the same column with the same letter are not significantly different ($p<0.05$).

Table 2-6. Effect of defoliation technique, height of defoliation and corresponding interaction on least squares mean total pre and post-treatment production of alfalfa (SE=standard error, N=sample size).

Effect	**Comparison**	**Total Biomass (g DM/cm^2 crown area)**	**SE**	**N**
Defoliation technique	Mowed	0.84 a	.06	18
	Stripped	0.52 b	.06	18
Defoliation height	2.5cm	0.79 a	.07	12
	7.5cm	0.72 a	.07	12
	15cm	0.52 b	.07	12
Technique x height	Mowed to 2.5cm	1.00	.10	6
	Mowed to 7.5cm	0.87	.10	6
	Mowed to 15cm	0.64	.10	6
	Stripped to 2.5cm	0.57	.10	6
	Stripped to 7.5cm	0.57	.10	6
	Stripped to 15cm	0.40	.10	6

Within each effect, means in the same column with the same letter are not significantly different ($p<0.05$).

2.3.3 Primary and Secondary Stem Density

Analysis of the post-treatment stand revealed the mean density of primary (crown-derived) stems was greater ($p<0.05$) in plants defoliated by mowing than by stripping

(Table 2-7). Other effects on primary stem density were not significant ($p>0.05$). There were no main effects on secondary stem density ($p>0.05$), but a defoliation technique by height interaction was apparent ($p<0.05$). Plants mowed to a 2.5cm height had fewer secondary stems than plants mowed to 15cm with all other treatments intermediate in secondary stem density. Although measures of stem density were made on post-treatment plants in their above-ground entirety, and therefore a portion of stems was pre-treatment carryover, it was visually apparent that post-treatment stem counts were additive to stems remaining after treatment application. Mowed stem carryover was visually identifiable by the obvious appearance of the previously cut stems, while stripped stem carryover was easily distinguished by minor scrape damage to external stem tissue resulting from the stripping treatment application.

Table 2-7. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean density of primary and secondary stems of post-treatment alfalfa (SE=standard error, N=sample size).

Effect	**Comparison**	**Primary Density (stems/cm^2 of crown)**	**SE**	**Secondary Density (stems/cm^2 of crown)**	**SE**	**N**
Defoliation technique	Mowed	1.88 a	0.16	1.90	0.19	18
	Stripped	1.49 b	0.16	1.98	0.19	18
Defoliation height	2.5cm	1.65	0.20	1.51	0.23	12
	7.5cm	1.89	0.20	2.13	0.23	12
	15cm	1.52	0.20	2.19	0.23	12
Technique x Height	Mowed to 2.5cm	1.73	0.28	1.04 a	0.28	6
	Mowed to 7.5cm	2.23	0.28	2.11 ab	0.28	6
	Mowed to 15cm	1.68	0.28	2.57 b	0.28	6
	Stripped to 2.5cm	1.57	0.28	1.98 ab	0.28	6
	Stripped to 7.5cm	1.55	0.28	2.15 ab	0.28	6
	Stripped to 15cm	1.35	0.28	1.80 ab	0.28	6

Within each effect, means in the same column with the same letter are not significantly different ($p<0.05$).

2.3.4 Height of Origin of Secondary Stems

The mean height of origin of secondary stems above the root crown was taller ($p<0.01$) for plants defoliated by stripping than by mowing, and was taller ($p<0.001$) as defoliation height increased (Table 2-8). A defoliation technique by height effect was also apparent ($p<0.05$) with mean height of origin ranging from a low of 1.1cm above the crown in plants mowed to a 2.5cm height, to a high of 9.8cm above the crown in plants stripped to a 15cm height.

Table 2-8. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean height of secondary stem origin of post-treatment alfalfa (SE=standard error, N=sample size).

Effect	Comparison	Height Above Top of Crown (cm)	SE	N
Defoliation technique	Mowed	4.4 a	0.2	568
	Stripped	7.3 b	0.2	655
Defoliation height	2.5cm	3.5 a	0.2	358
	7.5cm	5.2 b	0.2	366
	15cm	8.9 c	0.2	499
Technique x Height	Mowed to 2.5cm	1.1 a	0.4	123
	Mowed to 7.5cm	4.3 b	0.3	187
	Mowed to 15cm	8.0 cd	0.3	258
	Stripped to 2.5cm	5.9 b	0.3	235
	Stripped to 7.5cm	6.2 bc	0.3	179
	Stripped to 15cm	9.8 d	0.3	241

Within each effect, means in the same column with the same letter are not significantly different ($p<0.05$).

2.3.5 Forage Quality

Crude protein (CP) and neutral detergent fibre (NDF) were measures of forage quality performed on total post-treatment herbaceous biomass (Table 2-9), thereby excluding biomass removed from plants during treatment application. CP and NDF content of herbage were higher ($p<0.05$) and lower ($p<0.05$), respectively, for mowed than stripped plants. CP was also highest for plants defoliated to a 2.5cm height ($p<0.01$) while other effects were not significant ($p>0.05$) for CP and NDF.

Table 2-9. Effect of defoliation technique, height of defoliation, and corresponding interaction on least squares mean crude protein (CP) and neutral detergent fiber (NDF) content of post-treatment alfalfa (SE=standard error, N=sample size).

Effect	Comparison	CP (%)	SE	NDF (%)	SE	N
Defoliation technique	Mowed	25.4 a	0.2	35.1 a	0.6	18
	Stripped	24.0 b	0.2	38.0 b	0.6	18
Defoliation height	2.5cm	26.6 a	0.3	35.0 a	0.7	12
	7.5cm	24.1 b	0.3	36.8 a	0.7	12
	15cm	23.4 b	0.3	37.9 a	0.7	12
Technique x Height	Mowed to 2.5cm	28.1	0.4	31.9	1.1	6
	Mowed to 7.5cm	24.6	0.4	36.4	1.1	6
	Mowed to 15cm	23.5	0.4	37.1	1.1	6
	Stripped to 2.5cm	24.9	0.4	38.2	1.1	6
	Stripped to 7.5cm	23.6	0.4	37.2	1.1	6
	Stripped to 15cm	23.3	0.4	38.7	1.1	6

Within each effect, means in the same column with the same letter are not significantly different ($p<0.05$).

2.4 Discussion

2.4.1 Regrowth Period

In this experiment, the regrowth period required for alfalfa to reach the state of a harvestable stand (see 2.2.6 above) after treatment was 5 days longer ($p<.001$) for mowed alfalfa than for stripped alfalfa and was 10 days longer at a 2.5cm defoliation height than at 15cm (Table 2-4). This reflects the greater amounts of forage biomass removed at treatment application in mowed versus stripped treatments, and at shorter versus taller defoliation heights. Raw mean forage dry matter removed at time of treatment averaged 74 and 47% across mowed and stripped treatments, respectively; and removal averaged 45, 59 and 63% across treatments defoliated at 2.5, 7.5 and 15cm heights, respectively. As a result, greater residual biomass was carried over from treatment application in stripped stands and in stands with taller defoliation heights, and this carryover contributed directly to early attainment of post-treatment harvest criteria for those treatments. These observations support those of Leach (1968, 1979) and others (Sheaffer et al. 1988) who state the advantage of leaving taller stubble post-cutting is that there are more sites available for initiation of regrowth. It follows that while the rate of regrowth in a taller "stripped" stubble may not be greater than in "mowed" stubble due to shading or hormonal inhibition of new crown shoots (Leach 1968, 1979), the recovery to a harvestable state may be quicker because less root TNC (total nonstructural carbohydrates) and N (nitrogen) reserves need be mobilized to support regrowth than in shorter "mowed" stubble where regrowth is predominantly crown bud-derived and where less photosynthetically active biomass remains to contribute to regrowth (Avice et al. 1996; Barber et al. 1996; Volenec et al. 1996).

2.4.2 Regrowth and Total Herbaceous Biomass

The amount of regrowth biomass required to attain harvest criteria was necessarily greater ($p<0.05$) in mowed than in stripped alfalfa because of lesser residual carryover in the former (Table 2-5). Accordingly, total herbaceous biomass production (which included regrowth plus carryover plus all biomass removed at initial treatment) was greater ($p<0.05$) in mowed than stripped alfalfa (Table 2-6), though the extra regrowth required to reach a harvestable state resulted in a longer recovery period. These results indicate alfalfa was able to recover to a harvestable state regardless of defoliation method. Furthermore, defoliation height was negatively related to total biomass production with a similar trend apparent for regrowth biomass. This is consistent with previous reports that higher herbage yields are obtained with shorter versus taller defoliation heights (Sheaffer et al. 1988), presumeably because stems originating from axillary buds on old stems contribute less to herbage regrowth than stems originating from crown buds (Wolf and Blaser 1981). Furthermore, the contributions of residual stubble to regrowth has been questioned in that if photosynthesis is slow in remaining stubble, or shades the plant base, it may inhibit crown shoot development (Leach 1968; Sheaffer et al. 1988). This would likely be the case for stripped treatments, wherein most remaining stubble was predominantly stemmy material, and photosynthetic production in stems is known to be about 1/3 that of leaves (Heichel et al. 1988).

2.4.3 Primary and Secondary Stem Density

Primary stem density was greater ($p<0.05$) in mowed than in stripped post-treatment alfalfa. This is consistent with reports indicating regrowth is increasingly crown-derived as residual biomass declines under progressively intensive defoliation (Leach 1968, 1979, Sheaffer et al. 1988). Unfortunately, in this experiment, analysis of stem densities in post-treatment alfalfa were inclusive of regrowth and residual stem carryover following treatment application. This limitation prevented quantitative separation of differences between pre and post-treatment primary stem densities.

I hypothesized that secondary stem densities would be greater in stripped than mowed alfalfa due to more axillary sites being available for regrowth in the taller residual stripped stubble. This did not occur. A study by Leach (1970a) may offer a partial explanation. Leach found nearly all regrowth shoots arose from very near the crown in alfalfa cut at 2, 5 or 10cm above the crown, thereby concluding that cutting at taller heights increased total shoot numbers only slightly. He submits nearly all regrowth shoots arise from very near the crown, either on the crown itself or within the first 2cm above it, and so defoliation at greater heights has little effect on axillary shoot numbers because many are effectively considered as being crown-derived. Furthermore, he reports most shoots arising from or near the crown will resume extension growth earlier, and therefore, grow larger than axillary-derived shoots at higher positions. This concurs with Wolf and Blaser (1981) and others (see Sheaffer et al. 1988) who report stems originating on axillary buds of old stems contribute less to regrowth than those originating from crown buds. Hence, most regrowth in stripped plants may have eminated from either crown-derived or axillary-derived stems located very near the crown. Based on this, lower position buds may have dominated the origin of most regrowth relative to the axillary buds on upper portions of stripped stems. Moreover, additional secondary stems produced on large crown-derived stems during regrowth likely helped offset differences in stem density expected from the carryover of secondary stems in stripped treatments. Unpublished data from this experiment support this theory in that no defoliation technique effect ($p>0.05$) was apparent for the relative contributions of crown-derived and axillary-derived biomass to overall post-treatment biomass. The same data also indicated crown-derived biomass made up the majority of post-treatment harvested material in all treatments of this experiment. Most crown-derived stems apparently took hormonal precedence as major sinks for photosynthates and organic root reserves and subsequently developed into new primary stems typically 20cm or more in length prior to post-treatment harvest. In contrast, most regrowth from axillary-derived stems was much less robust and commonly only 1-5cm in length. Hence, while secondary stem densities did not differ among defoliation techniques, mowed plants relied more on robust crown-derived stems for regrowth than did stripped plants. Furthermore, secondary stems on plants that were stripped were more spatially isolated above the crown as evidenced by a greater mean height of origin (Table 2-8) than in mowed plants. Considering the proximity and immediate access of crown-derived stems to the flow of uptake water, nutrients, and organic reserves from roots, it is logical that the portion of biomass originating from crown-derived primary stems exceeded that of axillary-derived stems, regardless of defoliation technique and resultant secondary stem densities.

A significant interaction occurred between defoliation technique and height whereby the combination of mowing alfalfa to a 2.5cm height resulted in fewer secondary stems than mowing to 15cm, while all other interaction means were not significantly different and intermediate in secondary stem density. This is consistent with reports by Fick et al. (1988) and others (Meyer and Larson 1975; Sheaffer et al. 1988) that the removal of axillary buds under progressively shorter cuttings reduces the number of axillary stems contributing to regrowth. However, Leach (1970a) reports that while the majority of regrowth in mowed plants comes from the crown, freshly initiated primary stems following intensive mowing will exhibit robust extension growth and become large dominant stems in the regrowth stand. Presumeably then, this robust growth compensates for fewer numbers of available sites for regrowth and less residual photosynthetically productive leaf area relative to plants mowed at taller heights.

2.4.4 Height of Origin of Secondary Stems

Measurement of the height of origin of all secondary stems on post-treatment alfalfa identified significant effects for defoliation method ($p<0.01$), defoliation height ($p<0.001$) and the defoliation method by height interaction ($p<0.05$). Mean height of origin of secondary stems was taller for stripped plants than for mowed plants, and was taller as defoliation height increased. Carryover of greater amounts of residual stem biomass in the taller stripped stubble contributed directly to this observation by contributing greater numbers of potential axillary sites for regrowth, regardless of the obvious differences in relative contributions to regrowth biomass of lower secondaries (greater) to upper secondaries (lesser) as previously described. Results in this experiment concur with previous studies reporting higher heights of origin for secondary stems in taller stubbles post-cutting. Watters and Henderlong (1978) report greater axillary stem numbers above 5cm following cutting at both 13 and 25cm heights while Cowett and Sprague (1962) report increased axillary bud and stem formation at cutting to a 7.5cm relative to a 2.5cm stubble.

2.4.5 Forage Quality

In this experiment, post-treatment harvested alfalfa included residual biomass carried through on plants from the date of treatment application. As such, effects on forage quality due to stubble carryover were apparent. Post-treatment forage exhibited a greater ($p<0.05$) fiber and lower ($p<0.05$) crude protein content in stripped than in mowed alfalfa, presumeably due to the greater carryover of stemmy residual material in stripped treatments. Alfalfa stems are known to be of lower forage quality and higher fiber content than plant tops or leaves (Leach 1970b; Buxton et al. 1985; Onstad and Fick 1983) and digestibility of stems declines at a faster rate than in leaves as maturity advances (Kilcher and Heinrichs 1974; Fick and Holthausen 1975; Buxton et al. 1985; Marten et al 1988). As stemmy residual biomass carryover in post-harvest stubble increases, forage quality declines (Kalu and Fick 1983; Wilman and Altimimi 1984; Sheaffer et al. 1988). Results in this experiment affirm these previous studies in that greater amounts of stem were carried over to post-treatment harvest in stripped treatments than in mowed treatments. Forage quality was also greater at the shortest defoliation height. These effects occurred in spite of the fact this experiment employed treatments at a mid-vegetative stage of growth when stems were still high in quality relative to later stages of growth (Marten et al. 1988), though residual stems were aging in post-treatment stubble. Applying treatments from this experiment at later stages of growth could be expected to result in even greater differences in forage quality in response to defoliation method and height (Sheaffer et al. 2000).

2.4.6 Residual Biomass

Numerous studies report that defoliation for progessively taller stubble increases the number of potential sites for regrowth and leaves behind greater residual and photosynthetically active phytomass to help fuel reqrowth than in shorter stubbles (Leach 1968, 1979; Wolf and Blaser 1981; Cralle and Heichel 1981, Gabrielson et al. 1985; Sheaffer et al. 1988). On that basis, and results in this experiment concur, leaving more residual biomass following defoliation leads to quicker plant recovery to a harvestable state. Further, stripping (grazing) would be expected to be less physiologically stressful to the plant than mowing, and taller stubbles less stressful than shorter stubbles following defoliation. However, others submit retention of residual biomass inhibits regrowth from new crown shoots by shading of the crown and hormonal inhibition of crown shoots (Leach 1979), as well as increased competition from residual weed biomass which accelerates plant loss and yield reduction in the stand over time (Belesky and Fedders 1997). Therefore, an opportunity cost results from harvesting less herbage production under defoliation treatments which are less severe. Furthermore, resultant greater shoot numbers under less severe defoliation may lead to increased intershoot competition for photosynthates produced after defoliation, for root N and TNC reserves, and result in the size of individual shoots being inversely related to shoot number or shoot die-back occurring (Heichel et al. 1988). Finally, in the context of recent research indicating the majority of reserves fueling regrowth comes from organic N supplies in the roots, and that residual biomass is of little consequence in directing photosynthate to new shoots (Ourry et al. 1994; Avice et al. 1997), there appears to be no great physiological benefit to plants in taller stands which are managed for carryover of large amounts of residual biomass. However, this carries the assumption that adequate recovery periods would be provided following more intensive levels of defoliation.

Consequently, alfalfa plant morphology which facilitates more complete defoliation by wapiti and reduced stubble carryover would be expected to maximize food consumption while minimizing stubble carryover. This implies alfalfa cultivars selected for a multifoliate growth habit, or thinner primary stems more readily severed by wapiti prehension, or selection for rapid regrowth from secondary stems following defoliation by wapiti, are likely to foster more efficient food intake rates. The grazing-tolerant cultivar used in this study (*Medicago sativa* L. cv. Alfagraze) has been described as having thick stems (Brummer and Bouton 1991), which could be expected to result in less stem breakage upon grazing by wapiti than other cultivars, and resultant greater stubble carryover. Hence, research on cultivar influences on foraging efficiency may be warranted. Also, alternative approaches to remove herbaceous residual carryover after wapiti grazing might include mowing the stand for hay, or implementing grazing by a consummate grazer like cattle or bison in a leader-follower grazing system.

2.5 Conclusions

Alfalfa proved very plastic in regrowth response to defoliation method and height. Stripped alfalfa exhibited quicker recovery to a harvestable state, but less regrowth biomass, and lower total forage yields than mowed alfalfa. Post-treatment biomass was predominantly crown-derived regardless of treatment but axillary-derived material was an important secondary source of biomass. Defoliation at taller rather than shorter heights resulted in quicker recovery to a harvestable state. Hypothesized greater secondary stem density under stripping was not apparent because substantial secondary stem regrowth occurred from large post-treatment crown-derived stems in mowed alfalfa. Forage quality was lower in stripped versus mowed treatments and at progressively taller defoliation heights. This was attributed to greater amounts of residual stemmy material being carried through to harvest after treatment application.

Some implications for grazing management of wapiti were apparent from this experiment. There were no apparent benefits to post-treatment wapiti food quality or quantity attributable to stripping rather than mowing, other than a quicker recovery to a harvestable (grazeable) state. However, this statement applied only to the post-treatment stand, predominantly leafy material removed by stripping would be expected to be higher quality wapiti food than the combined pool of stem and leaf removed by mowing. This leads to speculation that graziers could insure high quality food intake for wapiti by allowing animals to strip high quality foods, then subsequently return to the stand after a short regrowth period to strip more high quality feed. However, that approach carries a significant opportunity cost in forage which could otherwise be harvested by simply cutting the post-grazed stand for hay to remove residual stem carryover and foster fresh crown-derived regrowth. The underlying question of whether it would be a better strategy to regraze the stand or mow it for hay production is speculative, beyond the scope of this experiment, and would require an assessment of wapiti nutritional needs during the growing season, availability and costs of alternate summer feeds, and other animal management factors.

In summary, mowing at some point after wapiti grazing would be recommended to facilitate removal of residual stem material and to foster subsequent crown-derived regrowth of maximal quality and quantity. Where wapiti pasture is required, alternating grazing with mowing or mowing after grazing to remove residual stem would promote greater quantity and quality of herbaceous regrowth and total biomass produced and harvested.

2.6 References

Agriculture Canada. 1988. Soil Landscapes of Canada: Alberta. Canada Soil Inventory, Land Resource Research Centre, Research Branch, Agriculture Canada Publication 5237/B. Supply and Services Canada. 8 pp., 2 maps.

Allen, V.G. 1985. Alfalfa management for hay and pasture. p. 5-8. In: Proc. 41st Southern Pasture Improve. Conf., Raleigh, N.C. 20-22 May, 1985. USDA-ARS. U.S. Gov. Print. Office, Washington, DC.

AOAC (Association of Official Analytical Chemists). 1990. Protein (crude) in animal feed, copper sulfate/titanium dioxide mixed catalyst Kjeldahl method. 988.05 p.70. In: Official Methods of Analysis of the AOAC. Fifteenth Edition.

Avice, J.C., A. Ourry, G. Lemaire, J.J. Volenec and J. Boucaud. 1997. Root protein and vegetative storage protein are key organic nutrients for alfalfa shoot regrowth. Crop Sci. 37:1187-1193.

Barber, L.D., B.C. Joern, J.J. Volenec and S.M. Cunningham. 1996. Effects of supplemental nitrogen on alfalfa regrowth and taproot nitrogen mobilization. Crop Sci. 36:1217-1223.

Belesky, D.P. and J.M. Fetters. 1997. Residue height influences stand dynamics of alfalfa grown on a shallow soil. Agron. J. 89:975-980.

Bouton, J.H., S.R. Smith, Jr., D.T. Wood, C.S. Hoveland, and E.C. Brummer. 1991. Registration of 'Alfagraze' alfalfa. Crop Sci. 31:479.

Brummer, E.C. and J.H. Bouton. 1991. Plant traits associated with grazing-tolerant alfalfa. Agron. J. 83:996-1000.

Brummer, E.C. and J.H. Bouton. 1992. Physiological traits associated with grazing-tolerant alfalfa. Agron. J. 84:138-143.

Buxton, D.R., J.S. Hornstein, W.F. Wedin, and G.C. Marten. 1985. Forage quality in stratified canopies of alfalfa, birdsfoot trefoil, and red clover. Crop Sci. 25:273-279.

Cook, C.W. and J. Stubbendieck. 1986. Range research: basic problems and techniques. Soc. Range Management. Denver. Colorado. 317pp.

Counce, P.A., J.H. Bouton, and R.H. Brown. 1984. Screening and characterizing alfalfa for persistence under mowing and continuous grazing. Crop Sci. 24:282-285.

Cowett, E.R. and M.A. Sprague. 1962. Factors affecting tillering in alfalfa. Agron. J. 54:294-297.

Cralle, H.T. and G.H. Heichel. 1981. Nitrogen fixation and vegetative regrowth of alfalfa and birdsfoot trefoil after successive harvests or floral debudding. Plant Physiol. 67:898-905.

Environment Canada. 1993. Environment Canada Atmospheric Environment Service Canadian Climate Normals: Prairie Provinces 1961-90. Ministry of Supply and Services Canada. 266pp.

Environment Canada. 1999. Environment Canada Atmospheric Environment Service Climatological Station Register at Fabyan North. July 1, 1995 to September 30, 1999. 54pp.

Fick, G.W. and R.S. Holthausen. 1975. Significance of parts other than blades and stems in leaf-stem separations of alfalfa herbage. Crop Sci. 15:259-262.

Fick, G.W., D.A. Holt and D.G. Lugg. 1988. Environmental physiology and crop growth. p. 163-194. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Gabrielson, B.C., D.H. Smith and C.E. Townsend. 1985. Cicer milkvetch and alfalfa as influenced by two cutting schedules. Agron. J. 77:416-422.

Gordon, I.J. and A.W. Illius. 1988. Incisor arcade structure and diet selection in ruminants. Functional Ecology 2:15-22.

Haigh, J.C. and R.J. Hudson. 1993. Farming wapiti and red deer. Mosby Year-Book, Inc. St. Louis, Missouri. 369 pp.

Heichel, G.H., R.H. Delaney and H.T. Cralle. 1988. Carbon assimilation, partitioning, and utilization. p. 195-228. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Heinrichs, D.H. 1963. Creeping alfalfas. Adv. Agron. 15:317-337.

Heinrichs, D.H. 1978. The future of alfalfa for pasture in dry regions and research requirements. p. 4-9. In: D.K. Barnes (ed.). Report of the 26th Alfalfa Improvement Conf., Brookings S.D. 6-8 June, 1978. USDA-ARS, St. Paul, MN.

Hicks, C.R. 1973. Fixed, random and mixed models. p.173-187. In: Fundamental concepts in the design of experiments. Second Edition. Holt, Rinehart and Winston. New York. 349 pp.

Hoffman, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

Hudson, R.J. and M.T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. J. Range Manage. 38:80-82.

Janis, C.M. and D. Ehrhardt. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zool. J. Linnean Society 92:267-284.

Jiang, Z. and R.J. Hudson. 1993. Foraging postures of wapiti (*Cervus elaphus*). Appl. Anim. Behav. Sci. 36:275-287.

Jiang, Z. and R.J. Hudson. 1994. Bite characteristics of wapiti (*Cervus elaphus*) in seasonal *Bromus-Poa* swards. J. Range Manage. 47:127-132.

Kalu, B.A. and G.W. Fick. 1983. Morphological stages of development as a predictor of alfalfa herbage quality. Crop Sci. 23:1167-1172.

Kilcher, M.R. and D.H. Heinrichs. 1974. Contribution of stems and leaves to the yield and nutrient level of irrigated alfalfa at different stages of development. Can. J. Plant Sci. 54:739-742.

Laca, E.A., E.D. Ungar, N. Seligman and M.W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science 47:91-102.

Leach, G.J. 1968. The growth of the lucerne plant after defoliation: the effect of defoliation at different stages of maturity and at different intensities. Aust. J. Agric. Res. 19:517-530.

Leach, G.J. 1970a. Shoot growth on lucerne plants cut at different heights. Aust. J. Agric. Res. 21:583-591.

Leach, G.J. 1970b. Yield and chemical composition of leaves and stems of alfalfa at intervals up the shoots. J. Agric. Food Chem. 18:652-656.

Leach, G.J. 1979. Regrowth characteristics of lucerne under different systems of grazing management. Aust. J. Agric. Res. 30:445-465.

Marten, G.C., D.R. Buxton and R.F. Barnes. 1988. Feeding value (forage quality). p. 463-491. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Meyer, D.W. and K.L. Larson. 1975. Alfalfa management in North Dakota. North Dak. Farm Res. 32:3-9.

Onstad, D.W. and G.W. Fick. 1983. Predicting crude protein, in vitro true digestibility, and leaf proportion in alfalfa herbage. Crop Sci. 23:961-964.

Ourry, A., T.H. Kim and J. Boucaud. 1994. Nitrogen reserve mobilization during regrowth of *Medicago sativa* L.: Relationships between their availability and regrowth yield. Plant Physiol. 105:831-837.

Sheaffer, C.C., G.D. Lacefield and V.L. Marble. 1988. Defoliation schedules and stands. p. 411-438. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Sheaffer, C.C, N.P. Martin, J.F.S. Lamb, G.R. Cuomo, J. Grimsbo-Jewett, and S.R. Quering. 2000. Leaf and stem properties of alfalfa entries. Agron. J. 92:733-739.

Singh, Y. and J.E. Winch. 1974. Morphological development of 2 alfalfa cultivars under various harvesting schedules. Can. J. Plant Sci. 54:79-87.

Smith, S.R., Jr. and J.H. Bouton. 1993. Selection within alfalfa cultivars for persistence under continuous stocking. Crop Sci. 33:1321-1328.

Smith, S.R., Jr., J.H. Bouton and C.S. Hoveland. 1989. Alfalfa persistence and regrowth potential under continuous grazing. Agron. J. 81:960-965.

Smith, S.R., Jr., J.H. Bouton and C.S. Hoveland. 1992. Persistence of alfalfa under continuous grazing in pure stands and in mixtures with tall fescue. Crop Science 32:1259-1264.

SPSS Inc. 1999. SYSTAT 9 Statistics I. SPSS Inc. Chicago. IL. 660 pp.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife Publication T/245. Edmonton, Alberta, Canada. 59pp., 1 map.

Teuber, L.R. and M.A. Brick. 1988. Morphology and anatomy. p. 125-162. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Undersander, D., D.R. Mertens and N. Thiex. 1993a. Neutral detergent fibre-amylase procedure. Method 5.1. p.95-99. In: Forage analyses procedures . National Forage Testing Association. Omaha, Nebraska.

Undersander, D., D.R. Mertens and N. Thiex. 1993b. Standardizing alpha-amylase activity for neutral detergent fiber determination. Method 5.2. p.100-103. In: Forage analyses procedures . National Forage Testing Association. Omaha, Nebraska.

Vance, C.P., G.H. Heichel and D.A. Phillips. 1988. Nodulation and symbiotic dinitrogen fixation. p. 229-258. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Van Keuren, R.W. and A.G. Matches. 1988. Pasture production and utilization. p. 515-538. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s).

Volenec, J.J., A. Ourry and B.C. Joern. 1996. A role for nitrogen reserves in forage regrowth and stress tolerance. Physiol. Plant. 97:185-193.

Willms, W. 1978. Foraging strategy of ruminants. Rangeman's Journal 5(3):72-74.

Wilman, David and M.A.K. Altimimi. 1984. The in-vitro digestibility and chemical composition of plant parts in white clover, red clover and Lucerne during primary growth. J. Sci. Food Agric. 35: 133-138.

Wolf, D.D. and R.E. Blaser. 1981. Flexible alfalfa management: early spring utilization. Crop Sci. 21:90-93.

Wolf, D.D. and V.G. Allen. 1990. Yield and regrowth characteristics of alfalfa grazed by steers during spring and summer. Agron. J. 82:1079-1082.

Watters, V.L. and P.R. Henderlong. 1978. Alfalfa regrowth morphology and TNC changes with increased defoliation height and frequency. Agron. Abstr. Amer. Soc. of Agronomy. Madison. WI. p.106.

Wonders, W.C. 1969. Atlas of Alberta. Government of Alberta and Univ. of Alberta. Edmonton, Alberta, Canada.

3.0 EFFECT OF SWARD MANAGEMENT SYSTEMS ON ALFALFA REGROWTH POTENTIAL

3.1 Introduction

Renecker (1988) and Hudson and Adamczewski (1990) describe many practical aspects of wapiti (*Cervus elaphus*) farming in Canada including management of farmed herds at greater stocking densities than in wild populations. This move towards intensive management has been reinforced by stringent government regulations dictating the licensing and designation of lands used for cervid farming, a government-administered animal inventory system, and laws requiring tall and expensive paige-wire fences on cervid farms (Province of Alberta 1994). As a result, most Albertan and other Canadian wapiti farms have been developed on lands once used for cattle pasture or cultivated cropland which are typically less expensive to fence and more productive than marginal lands (Renecker 1988). Pastures are a primary source of food for wapiti during the growing season with alfalfa (*Medicago sativa*) and other legumes used as major components of tame pasture stands (Thorleifson 2001). Canadian wapiti farmers commonly employ 50 to 80% (up to 100%) alfalfa in pasture stands because of the high quality forage produced and the minimal risk for bloat relative to conventional livestock (Haigh and Hudson 1993; Klein 1997). As a result, studies of alfalfa persistence under grazing are of great practical importance to wapiti farmers. Most grazing-tolerant alfalfa cultivars in North America have been selected for broad crowns or creeping rootedness (ie. the ability to initiate new shoots from lateral roots) (Heinrichs 1963, 1978; Brummer and Bouton 1991); and more recently, for persistence under continuous stocking by cattle, prolific fall budding, decumbent growth habit, stubble leaf area retention, early fall dormancy, deep-set crown development and the ability to maintain root carbohydrate levels under grazing (Smith et al. 1989, 1992; Wolf and Allen 1990; Bouton et al. 1991; Smith and Bouton 1993).

Taproot carbohydrate levels have been widely accepted as the predominant factor affecting legume persistence and regrowth after defoliation (Graber et al. 1927; Smith 1962, 1964; Heichel et al. 1988), but more recent studies have assigned equal or greater importance to the role of N reserves (Volenec et al. 1996; Avice et al. 1997; Kalengamaliro et al. 1997; Cunningham et al. 1998). Although it has been known for many years that shoot recovery after defoliation involves carbohydrate mobilization from remaining source tissues, recent studies indicate the majority of C is used in root respiration (Avice et al. 1996), while root organic N supplies are more specifically mobilized in support of regrowing shoots and leaves (Kim et al. 1991, 1993; Ourry et al. 1994; Volenec et al. 1996). In most forage species, N reserves are mainly of organic form with protein-N constituting the largest pool and amino acid-N as the most readily mobilized from source to sink tissues (Ourry et al. 1989; Volenec et al. 1996). In alfalfa, three taproot polypeptides of molecular masses of 15, 19 and 32 kiloDaltons act as VSP (vegetative storage proteins) as described by Hendershot and Volenec (1993a,b). These polypeptides meet several criteria useful for defining VSP (Cyr and Bewley 1990; Staswick 1994). They represent a large proportion of the soluble protein pool and exhibit a cyclic pattern of synthesis-degradation-mobilization following defoliation (Hendershot and Volenec 1993b) or spring growth (Hendershot and Volenec 1993a). Mobilization of amino acids resulting from VSP degradation represents the chief form of N transported from sources to sinks (Ourry et al. 1989; Volenec et al. 1996). In summary, VSPs are considered to be proteins that are preferentially synthesized during development of storage organs, then are depleted from storage organs during reactivation of meristems. VSP abundance greatly exceeds other proteins in perennating organs, and generally act as a reservoir of N for situations where N requirements of a plant cannot be met by root uptake of N or N_2 fixation (Cyr and Bewley 1990; Cunningham et al. 1998).

Pastures on Canadian wapiti farms are often alternated between use by wapiti and cutting for hay. This is because pastures that are overmature or predominantly comprised of coarse stemmy material after grazing by wapiti in late spring-early summer, or pastures planned for use in breeding season, are often cut for hay in summer to initiate high quality regrowth prior to rut (Klein 1997). Maintenance of high quality pasture in late summer helps insure maximal conception rates during the fall breeding season (Haigh and Hudson 1993). Harvested hay is typically used for winter feed (Fargey 1987) with supplemental feeding programs on western Canadian wapiti farms beginning about November and ending in mid to late April (Renecker 1988). As a result, wapiti farmers are commonly faced with a managerial balancing act of manipulating the timing and intensity of grazing by wapiti and deciding when to cut paddocks for hay in order to maximize regrowth quality leading into the critical fall breeding season. Furthermore, it is common to observe pastures where grazing precedes haying and vice versa, as well as other pastures in critical handling or watering areas where grazing is largely continuous during the growing season. As a result, studies of varied sward management systems are of great practical interest with regards to their effects on alfalfa production and regrowth potential.

This experiment assessed the effects of four sward management systems (SMS) or treatments on the regrowth potential of a mature alfalfa stand. The impacts of the four treatments which employed various combinations of haying and wapiti grazing were studied over an entire growing season. Treatments were designed to collectively reflect the previously described variety in haying and grazing periods and intensities on western Canadian wapiti farms ranging from a near-continuous grazing system to a two-cut haying system. I hypothesized that the GZGZ (graze, graze) treatment which simulated near-continuous grazing for a significant portion of the growing season would have the severest physiological effect on alfalfa regrowth potential. At the other extreme, I hypothesized the HYHY (hay, hay) treatment (which simulated a two-cut haying system) would be least severe on alfalfa because this system employed cutting dates and recovery periods commonly recommended as best practice management (Sheaffer et al. 1988). I hypothesized the remaining two treatments GZHY (graze, hay) and HYGZ (hay, graze) would be intermediate in severity of effect on alfalfa based on inclusion of both grazing and haying components within these systems. Dependent variables used to measure alfalfa regrowth potential included root soluble protein, root TNC (total nonstructural carbohydrates) and crown bud proliferation.

3.2 Materials and Methods

3.2.1 Experimental Area

The experiment was conducted at 53° 03' 30" North, 110° 51' 30" West near Vermilion, in east central Alberta, Canada. The site contained loam textured Orthic Black Chernozemic soils on a morainal parent material with level to gently undulating surface expression (Agriculture Canada 1988) and was situated in the Aspen Parkland ecoregion of Alberta which has been described climatically and ecologically as a transition zone between boreal forest and grassland environments (Strong and Leggat 1992). The ecoregion is characterized by a cool, continental climate with short, warm summers and long, cold winters (Wonders 1969). Total annual precipitation for the ecoregion is normally 412mm with a median summer precipitation of 259mm where the majority of precipitation falls in June and July (Strong and Leggat 1992). Prior to this experiment, the site was cultivated for about 60 years and was part of a mixed farming operation dominated by cereal crops and mixed tame pasture.

The experimental site was located and fenced in April 1997 on a mature stand of alfalfa (*Medicago sativa* L. cv. Alfagraze) seeded in May 1992 at 9kg/ha (inoculated with *Rhizobium meliloti*) at a 15cm row spacing and subsequently cut for hay once annually to a height of 10cm between July 1-15 from 1993 to 1996 inclusive. Fertilizer was applied in a one-time deep banding operation prior to seeding in May 1992 at a rate of 30kg N ha^{-1}, 150kg P ha^{-1}, 20kg S ha^{-1}, and 20kg K ha^{-1}. Sethoxydim and 2,4-DB were applied to the entire site during the 1995 and 1996 growing season at rates of 556 and 1698 g ha^{-1} a.i., respectively, to eliminate grasses and non-leguminous weeds. Prior to initiating the experiment in 1997, plant species other than alfalfa were present in the stand at a combined total of <1% of above-ground biomass. This included dandelion (*Taraxacum officinale* Weber), yarrow (*Achillea millefolium* L.), aster (*Aster spp.*), northern bedstraw (*Galium boreale* L.) and foxtail barley (*Hordeum jubatum* L.). Stand composition was determined from four randomly selected 20 x 100cm clip plots of above-ground live herbaceous biomass taken from each paddock in the experimental site in late May, 1997, segregated by species, dried at 60°C for 48 hrs and weighed.

3.2.2 Climatological Data

Precipitation at the site was measured daily throughout 1997 using a cylindrical rain gauge graduated to 1mm. Precipitation events showing the distribution of rainfall during the growing season are depicted in Figure 3-1. Daily rainfall totals were pooled to determine total monthly precipitation for the experimental site as presented in Table 3-1. Long-term average monthly precipitation for two nearby Environment Canada weather stations (at Vermilion, about 30km north of the site, data from 1945-82; and at Fabyan North, about 11km southwest of the site, data from 1966-90) are also presented in Table 3-1 (Environment Canada 1993; Environment Canada 1999). Precipitation at the site in June, 1997, exceeded twice the long-term average monthly total (see Table 3-1) but this was followed by an extremely dry month of July where rainfall was 13% of the long-term average. Precipitation in August, 1997, was 77% of the long-term average, and in

September, 1997, precipitation exceeded the long-term average by 16%. The collective precipitation for the July through September period of 1997 was about 41% of the long-term average.

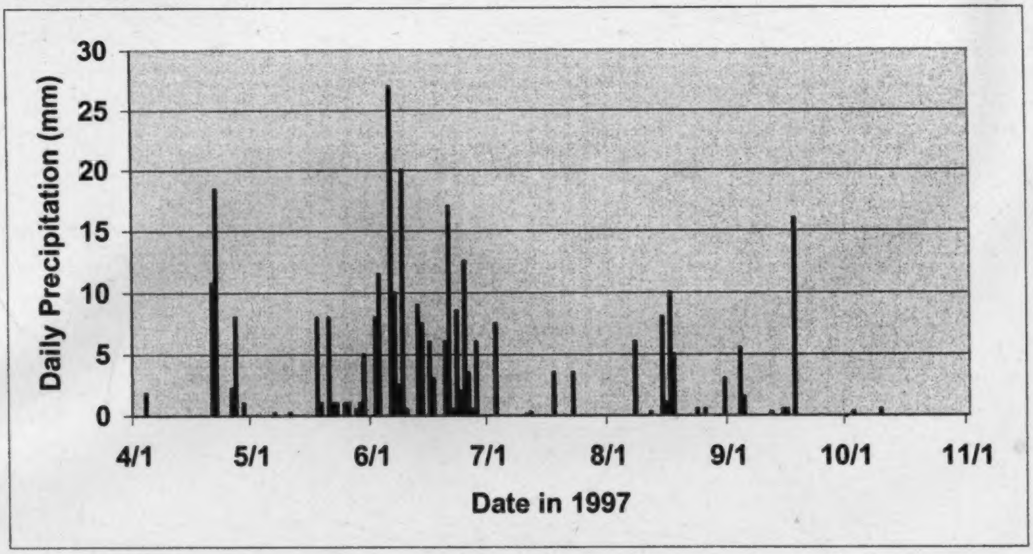


Figure 3-1. Total daily precipitation (mm) at the experimental site during the 1997 growing season.

Table 3-1. Monthly precipitation (mm) at study site for 1997 and long-term averages for nearby weather stations from 1945-82 and 1966-90.

Month	**Study Site 1997**	**Vermilion 1945-82**	**Fabyan 1966-90**
January	25.6	19.8	21.6
February	2.3	12.9	13.5
March	12.8	17.9	21.9
April	42.2	19.7	21.0
May	40.0	40.0	38.6
June	172.2	75.9	78.2
July	10.0	78.5	79.6
August	47.0	62.8	58.6
September	43.0	35.6	38.2
October	20.8	15.7	16.2
November	4.2	14.7	16.0
December	4.0	20.2	23.0
Total	424.1	413.7	426.5

Daily maximum and minimum temperatures were recorded at the experimental site during the growing season of 1997 and at the Environment Canada weather station at Fabyan North (Environment Canada 1999). These data were used to compute mean monthly maximum and minimum temperatures for the site in 1997 which are presented in

Table 3-2 with long-term averages for the Environment Canada weather station at Vermilion (Environment Canada 1993). A killing frost of -5°C occurred at the experimental site on October 6, 1997.

Table 3-2. Mean monthly maximum and minimum temperatures (°C) for 1997 and corresponding long-term averages from 1945-82.

Month	Max.1997	Min. 1997	Max. 1945-82	Min. 1945-82
January	-14.3	-25.8	-12.9	-23.7
February	-2.2	-14.2	-7.6	-19.1
March	-1.9	-12.6	-2.1	-13.6
April	7.0	5.5	9.2	-3
May	16.1	3.6	17.6	3.4
June	20.9	10.0	21.1	8.0
July	23.4	10.2	23.0	10.0
August	24.2	9.6	22.5	8.7
September	19.3	5.2	16.5	3.3
October	8.8	-2.7	10.8	-2.0
November	2.3	-8.0	-1.0	-11.0
December	0.5	-9.7	-9.6	-19.7

3.2.3 Experimental Design and Treatments

The experiment employed a randomized complete block design with two replicate blocks, each containing four 25 x 50m paddocks. One of four treatments (see Table 3-3) was applied to each paddock within a block on a randomly assigned basis (see Figure 3-2). Treatments were comprised of sward management systems made from variable combinations of grazing and haying typically found on wapiti farms in western Canada (Haigh and Hudson 1993).

Table 3-3. Description of the four treatments employed in 1997 (AUE was defined as an animal unit equivalent whereby one AUE equalled one-454kg nonlactating beef cow or the equivalent in wapiti liveweight; AUM was defined as the potential forage intake of one AUE for a period of one month).

Treatment	Description	Initiation Criteria	Stocking Density (AUE/ha)	Stocking Rate (AUM/ha)
GZHY	Grazed June 5-19 Hayed July 31	Grazed at mean height >25cm. Hayed at first flower.	32.4 na	16.2 na
HYGZ	Hayed July 2 Grazed July 31-August 16	Hayed at first flower. Grazed at first bud.	na 30.1	na 17.1
GZGZ	Grazed June 5-July 31 Grazed August 16-31	Grazed at mean height >25cm. Grazed at mean height >20cm.	17.4 19.2	33.1 9.6
HYHY	Hayed July 2 Hayed August 16	Hayed at first flower. Hayed at first flower.	na na	na na

Treatment applications were initiated based on plant morphological criteria assessed twice-weekly within each paddock using four randomly situated one-meter line transects. Along each transect, a vertical point frame was used to employ a first hits method at 10cm intervals as described by Cook and Stubbendieck (1986) to determine phenological stage of growth and mean sward height based on a total of 10 points per one meter transect. For each vertical point sampled, the first part of a plant contacted was designated as a "first hit", following which sward height above-ground level was estimated by measuring the maximal length of the primary stem attached to the first hit plant part. Phenological stage of growth of the plant for which the "first hit" occurred was recorded to verify attainment of initiation criteria. Grazing and haying components within each treatment were initiated when sward height or morphological criteria as specified in Table 3-3 were satisfied and indicative of the phenology where harvest by cutting or grazing is typically recommended (Sheaffer et al. 1988).

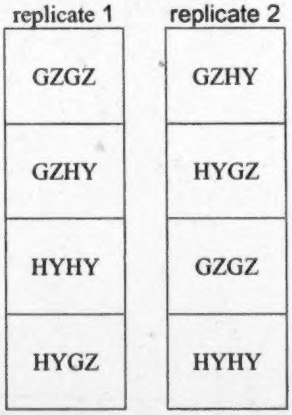


Figure 3-2. Field diagram of experimental design.

The experiment used a base herd of 24 female wapiti born in 1996 from which animals were randomly selected for use in grazing treatments. Prior to the experiment, in June 1997, animals weighed 181 ± 8 kg. Numbers of wapiti used for grazing components of the GZHY, HYGZ and GZGZ treatments were 10, 8 and 5, respectively. Those numbers were chosen based on estimates of paddock size, available herbaceous biomass, desired grazing periods and estimated daily consumption rates according to the method of Haigh and Hudson (1993). Wapiti were weighed before and after grazing treatments to allow calculation of mean stocking densities and rates as described in Table 3-3. The stocking rates employed in this experiment ranged from light to moderately heavy, based on reports by Mapfuomo et al. (2002) which associate light, moderate and heavy grazing with stocking rates of 20, 24, and 45 AUMs/ha, respectively.

3.2.4 Available Herbaceous Biomass

From late April to mid-October 1997, all live above-ground herbaceous biomass was harvested from four randomly selected 20 x 100cm clip plots within each treatment paddock inside each replicate on April 21, May 5 and 16, June 5 and 19, July 2, 3, 18 and

31, August 1, 16, 17 and 31, September 16, and October 10. Clip plots were randomly located at each sampling date. The original intent of the sampling scheme was designed to collect a labor-efficient time series analysis spanning the growing season at approximately two week intervals and to insure sampling dates included collections immediately prior to and following grazing and haying components of treatments. However, some samples were accidentally destroyed prior to data analysis resulting in the time series described above. All samples were oven dried at 60°C for 48 hrs and weighed.

Strategic timing of clip plot sampling dates at the start and end of each grazing and haying component within each treatment afforded crude estimates of herbaceous biomass removal (see Appendix 10). However, these estimates did not adjust for any growth or trampling which may have occurred during grazing periods in respective treatments.

3.2.5 Root Tissue Sampling

From late April to mid-October 1997, 2 to 5 roots were randomly selected and destructively collected by digging to a depth of 20cm using the method of Brummer and Bouton (1991) at each of four randomly selected locations within each treatment paddock on April 21, May 21, June 19, July 2 and 18, August 17 and October 10. The original sampling scheme was designed to collect a labor-efficient time series analysis spanning the growing season at about two week intervals but some samples were accidentally destroyed prior to data analysis. This resulted in a somewhat randomized sampling schedule that did not correspond perfectly to sampling dates for available herbaceous biomass.

Roots were packed in ice, transported to the laboratory where they were washed free of soil under cold water, measured for crown area and crown depth. Crown area was estimated as the product of two perpendicular measures of crown diameter following removal of vegetative biomass simulating the method of Brummer and Bouton (1991). Crown depth was measured as the distance from the upper limit of the crown to the uppermost point of the taproot as described by Teuber and Brick (1988). Taproots were severed from root crowns and trimmed to a standardized sampled root length of the uppermost 15cm of taproot using the method of Li et al. (1996) as preparation for chemical analyses. Uppermost taproot diameter was estimated as the mean of two ruler measurements on axes chosen by ocular approximation of minimum and maximum root diameter. Root samples were then cut into 1cm sections and placed in frozen storage until freeze drying, then ground in a Udy cyclone mill to pass a 1mm screen and returned to frozen storage until chemical analyses were performed.

For roots collected in the initial (April) and final (October) sampling dates, crown buds were counted concurrent with crown area and depth measurements. Crown buds were categorized as green (chlorophyll containing, frost sensitive) or white (non-chorophyll containing, frost tolerant) using the method of Cunningham et al. (1998). Post-treatment white bud counts in October were of specific interest as these frost tolerant buds are the structures from whence growth is initiated the following spring, barring winterkill

(McKenzie et al. 1988). White bud number per crown was standardized to three separate measures of bud density by using associated crown area, crown depth and taproot diameter measures as separate divisors of buds counted. This approach effectively adjusted for variability in the size of individual plants sampled from within the five year old stand in a manner similar to that of Brummer and Bouton (1991).

3.2.6 Chemical Analyses

All ground root samples were subsampled and analyzed for soluble protein using the method of Li et al. (1996). Proteins were extracted by suspending 25 mg of root tissue with an equal mass of polyvinylpolypryrolidone (PVPP, Sigma cat.#P-6755) in 750 μL of 100 mM imidazole-HCl buffer (pH 6.5) containing 10 mM 2-Mercaptoethanol in centrifuge tubes. Tubes were vortexed for 30 seconds, centrifuged at 3600 x *g* for 10 minutes and the supernatant retained. Samples were re-extracted and supernatants combined, then the concentration of soluble protein in the supernatant estimated using a Biorad protein determination kit (Bradford 1976).

Root samples collected at the final (October) sampling period were also subsampled and analyzed for TNC (total nonstructural carbohydrates) using the approach whereby %TNC = 100 – (crude protein + neutral detergent fiber + crude fat + ash). Crude protein was analyzed using a mixed catalyst Kjeldahl method (see method 988.05, AOAC 1990a) where subsamples were digested in sulfuric acid in the presence of a copper sulfate/titanium dioxide catalyst to convert organic nitrogen to ammonium sulfate, then ammonia from steam distilling titrated with a standard acid to derive nitrogen content and a 6.25 multiplier applied to estimate crude protein. Neutral detergent fiber (NDF) was analyzed using a NDF-amylase method (Undersander et al. 1993a, 1993b) whereby a neutral detergent solution was used to solubilize proteins and crude oils; EDTA was used to chelate calcium and remove pectins at boiling temperatures; and heat stable amylase used to remove starch. Crude fat was analyzed by exhaustively extracting root tissue with hexane, then distilling off hexane and weighing the remaining fat according to method 920.39 of AOAC (1990b). Ash content was estimated according to method 985.01 of AOAC (1990c) whereby ash content and carbon, sulfur and nitrogen content were determined using infrared radiation detection by a Leco 2000 Elemental Analyzer. This method measured carbon dioxide and sulfur dioxide emissions following combustion of a sample with pure oxygen while nitrogen measurements were made by thermal conductivity detection after combustion.

3.2.7 Statistical Analyses

Analysis of variance procedures in SYSTAT (SPSS Inc. 1999) were used to analyze data. Variation in dependent variables was partitioned into replicate (ie. block), treatment and sampling date main effects and corresponding interactions. Main effects and interactions of interest were tested with corresponding replicate interaction terms (see Appendices 11 to 17) according to the method of Hicks (1973). Where analysis of variance identified significant effects, individual degree of freedom orthogonal contrasts were conducted to confirm significance ($p<0.05$) of pairwise differences among means of main effects. Tukey's Studentized range statistic was used for comparison of means of significant ($p<0.05$) interactions. For graphic illustrations, 95% confidence intervals of means were estimated according to the method of Snedecor and Cochran (1967). Means separated by more than the 95% confidence interval were considered significantly ($p<0.05$) different.

3.3 Results

3.3.1 Available Herbaceous Biomass

Analysis of variance in available herbaceous biomass levels (see Appendix 11) showed significant differences among SMS treatments ($p<0.01$), sampling dates ($p<0.001$), and treatments by sampling dates ($p<0.001$). Comparisons of least squares means for main effects were not of great interest due to the asynchronous nature of treatment application. However, least squares means for each of the 56 treatment by sampling date interactions were presented as data points (with confidence intervals) in a time series progression in the upper portion of Figures 3-3 through 3-6. Presentation of interaction means in this manner facilitated visual comparison to changes in soluble root protein (see below) which was the dependent variable of primary interest. While all treatments showed spring (pre-treatment) and late summer (post-treatment) growth phases (Figures 3-3 through 3-6), biomass accumulation varied during the season in direct response to treatments.

Estimated total biomass removal was determined by simple difference between biomass clip plots taken at the start and end of each grazing and haying component within treatments. By this method, total biomass dry matter removed by grazing and haying was 4275, 4400, 2718, and 5838kg/ha within the GZHY, HYGZ, GZGZ and HYHY treatments, respectively (see Appendix 10). However, since exclosure cages were not present in the grazed pastures, these estimates did not adjust for growth that occurred during the grazing periods of the GZHY, HYGZ, and GZGZ treatments.

3.3.2 Soluble Root Protein

Analysis of variance in soluble root protein (see Appendix 12) showed significant differences among sampling dates ($p<0.001$) but no significant treatment ($p>0.05$) or treatment by sampling date ($p>0.05$) effects were evident. Least squares mean soluble protein content of roots across all four treatments peaked at 29.2g/kg prior to initiation of spring growth (Table 3-4), then declined to a mid-July low of 13.0g/kg which was roughly coincident with the midpoint in application of treatments, then exhibited post-treatment recovery during late summer and fall to 21.8g/kg by October 10. This final level was less than original pre-growing season levels but greater than the observed mid-summer lows. Although no significant treatment by sampling date effects were apparent, least squares interaction means were presented as data points (with confidence intervals) in a time series progression in the lower portion of Figures 3-3 through 3-6. These time series illustrate the progression of root protein levels in relation to available herbaceous biomass prior to, during, and after grazing and haying components of the four treatments.

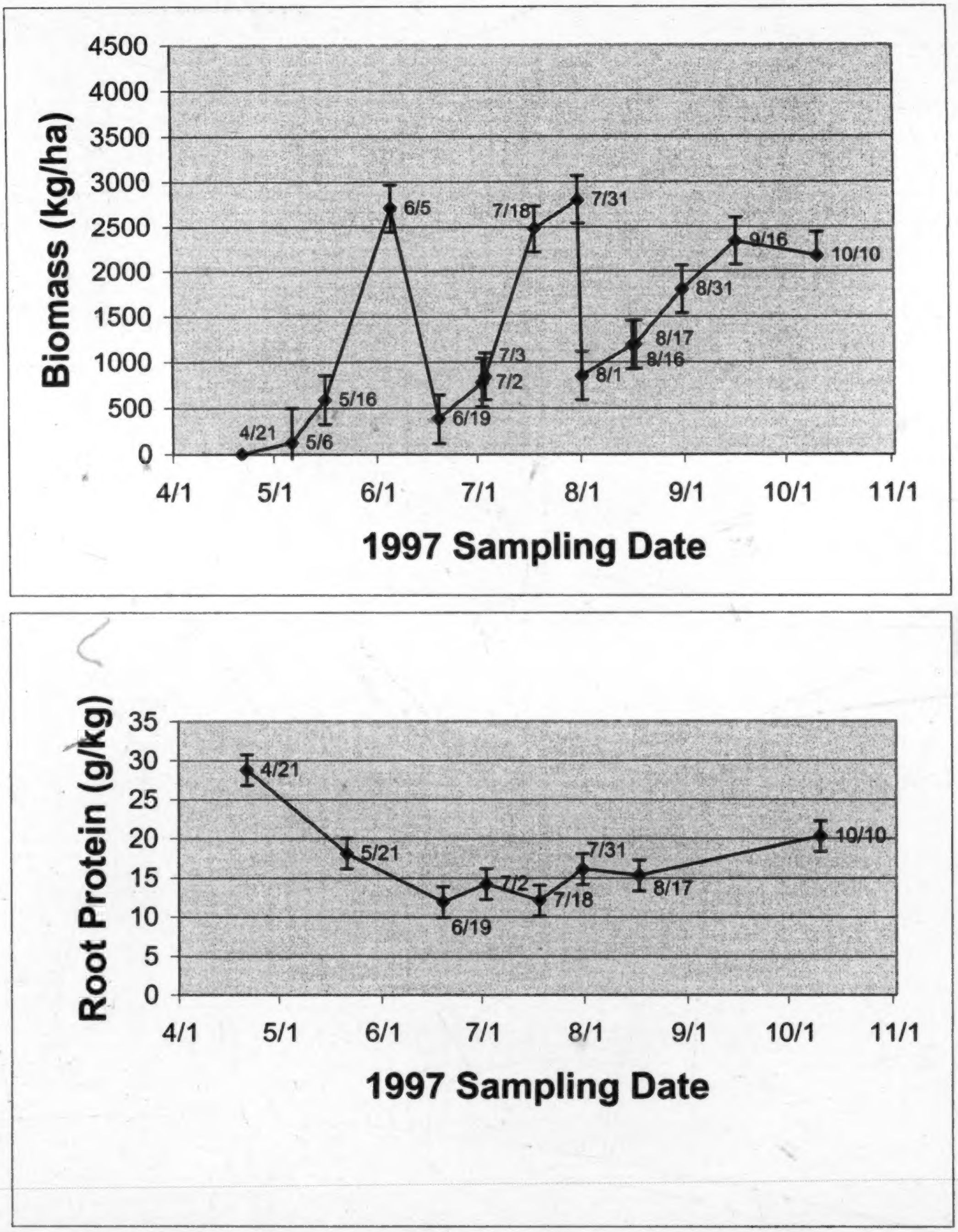


Figure 3-3. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the GZHY treatment (grazed 6/5 to 6/19, hayed 7/31) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.

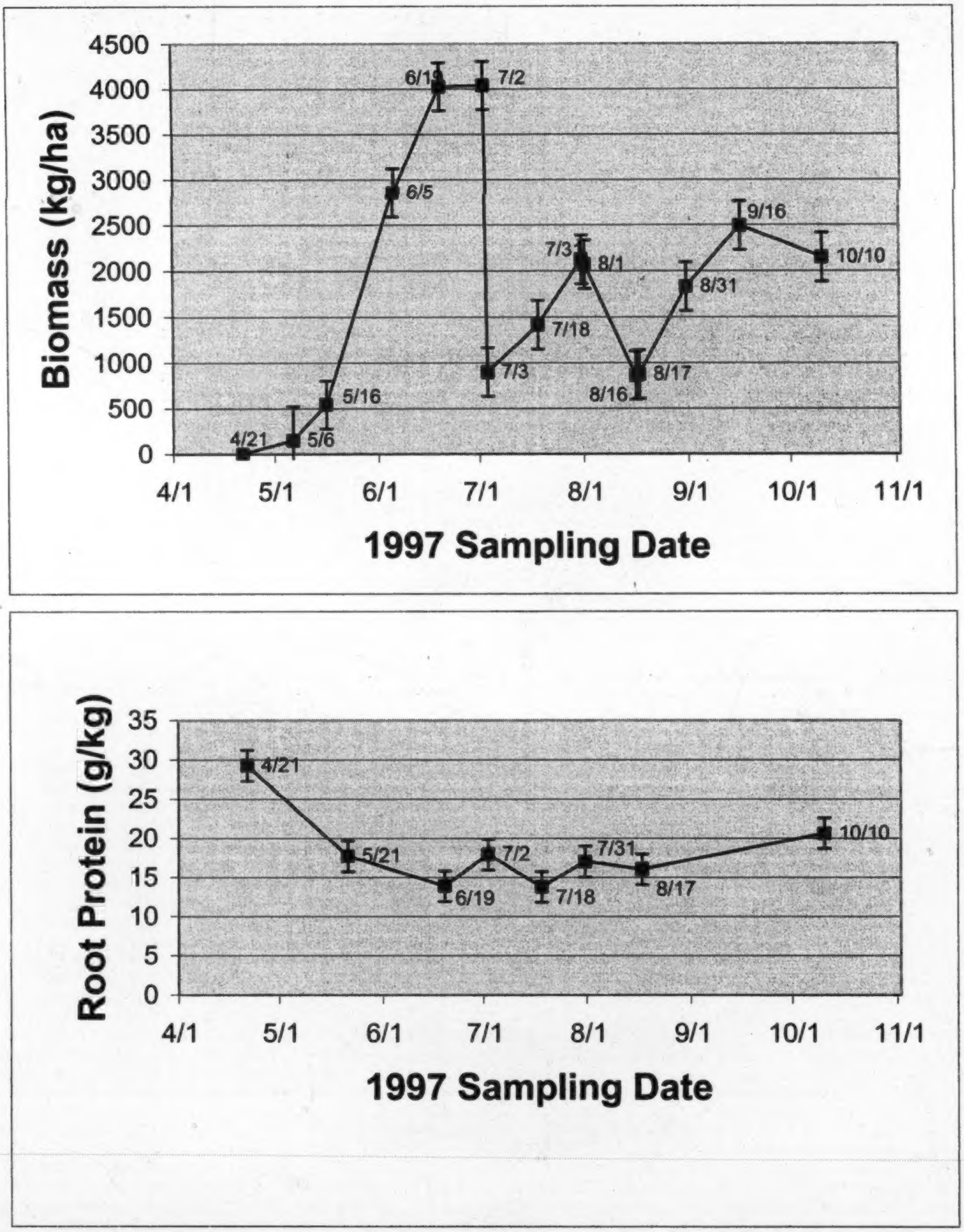
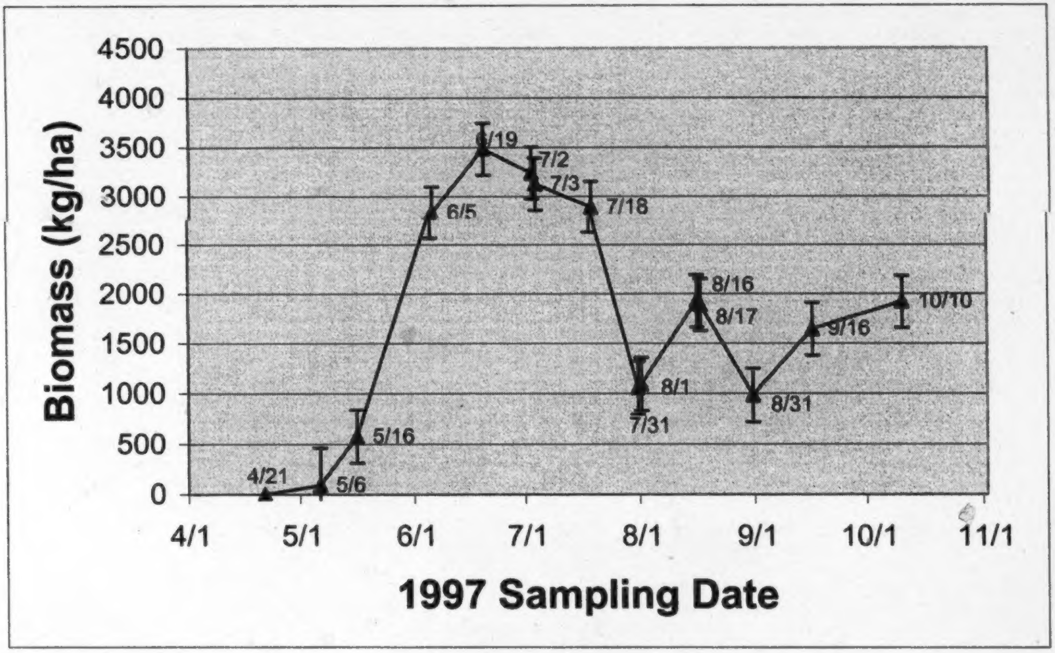


Figure 3-4. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the HYGZ treatment (hayed 7/2, grazed 7/31 to 8/16) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.



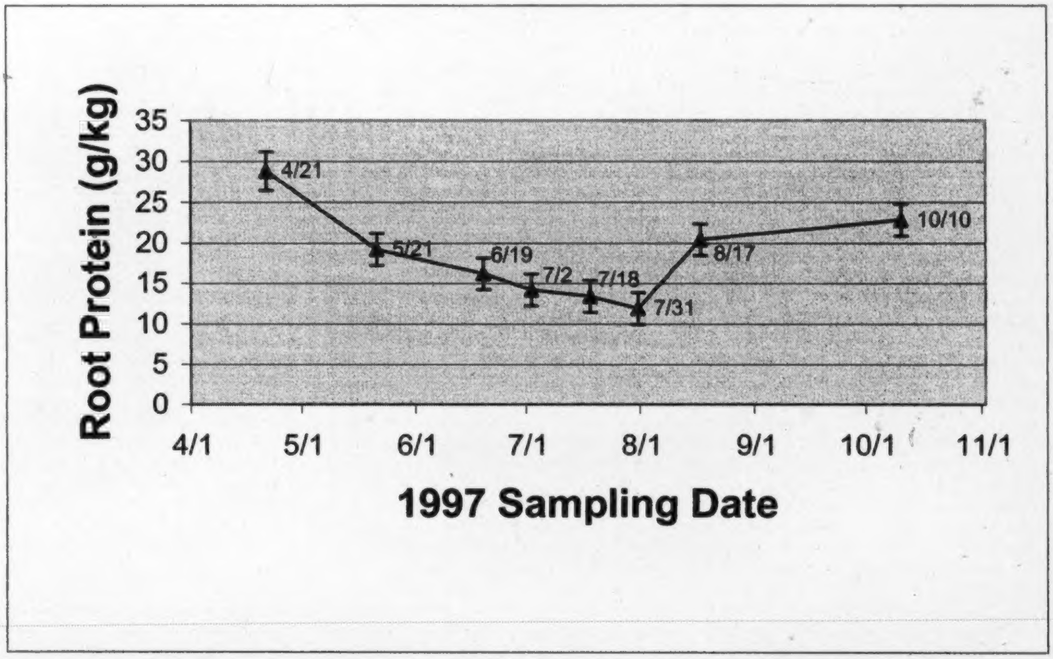


Figure 3-5. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the GZGZ treatment (grazed 6/5 to 7/31, grazed 8/16 to 8/31) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.

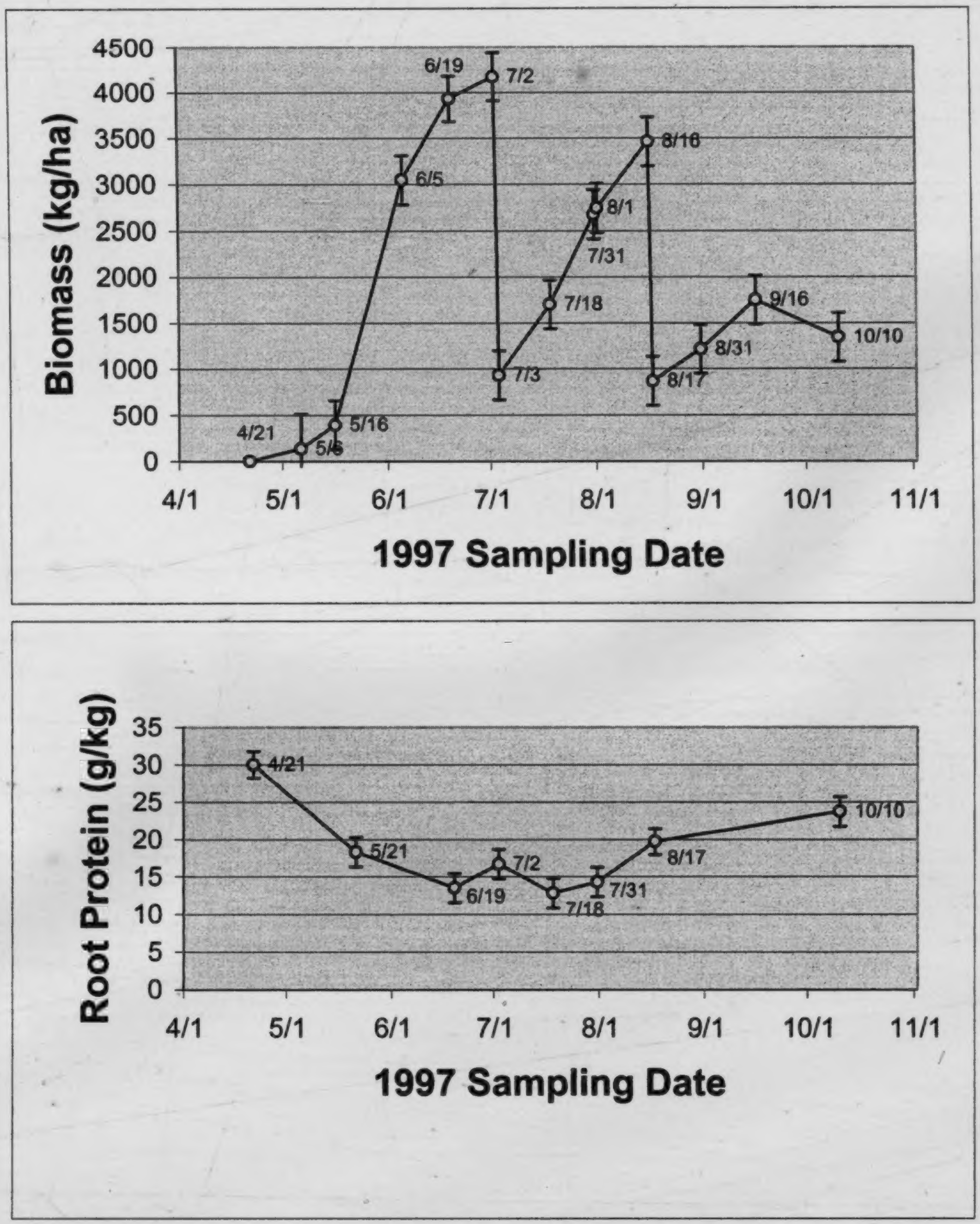


Figure 3-6. Changes in mean available herbaceous biomass (upper) and mean taproot soluble protein levels (lower) in alfalfa subjected to the HYHY treatment (hayed 7/2, hayed 8/16) during the 1997 growing season. Error bars represent 95% confidence limits and dependent variables are presented on a dry matter basis.

Table 3-4. Effect of sward management system and sampling date on least squares mean soluble protein content of alfalfa taproots (SE=standard error, N=sample size).

Effect	Treatment/Date	Root protein (g/kg DM)	SE	N
Sward Management System	GZHY	17.1 a	0.4	173
	HYGZ	18.2 a	0.4	161
	GZGZ	18.4 a	0.4	159
	HYHY	18.6 a	0.4	177
Sampling Date	April 21	29.2 a	0.5	82
	May 21	18.3 bc	0.5	80
	June 19	13.9 cd	0.5	83
	July 2	15.7 bc	0.5	85
	July 18	13.0 d	0.5	80
	July 31	14.8 c	0.5	80
	August 17	17.8 bc	0.5	92
	October 10	21.8 b	0.5	88

Within each effect, means in the same column with the same letter are not significantly different ($p<.05$).

In the GZHY treatment, soluble root protein declined from a high of 28.8 g/kg (SE=1.0) prior to the onset of spring growth to a low of 11.9g/kg (SE=1.0) at the end of the June 5 to 19 grazing period (Figure 3-3). Following removal of wapiti, root protein content recovered to 16.1g/kg (SE=1.0) prior to the July 31 hay treatment. This was followed by another increase in root protein during late summer-fall culminating at 20.3g/kg (SE=1.0) by October 10.

Under the HYGZ treatment, soluble root protein declined from a high of 29.3 g/kg (SE=1.1) prior to the onset of spring growth to a low of 13.9g/kg (SE=1.0) on June 19 (Figure 3-4). Protein then recovered to 17.9g/kg (SE=1.0) prior to the July 2 haying operation, then decreased to a level equivalent to the previous low by July 18. Following the grazing period, root protein levels recovered to 20.6g/kg (SE=1.0) by October 10.

The GZGZ treatment employed grazing continuously at a moderate stocking density from June 5 to July 31. Soluble root protein declined from a high of 28.8 g/kg (SE=1.2) prior to the onset of spring growth to a low of 11.9g/kg (SE=1.0) on July 31 which coincided with removal of wapiti (Figure 3-5). Protein then recovered to 20.4g/kg (SE=1.0) prior to the August 16-31 grazing period, and subsequently recovered to a statistically equivalent level of 22.8g/kg (SE=1.0) again by October 10.

Within the HYHY treatment, soluble root protein declined from a high of 30.0 g/kg (SE=0.9) prior to the onset of spring growth to a low of 13.5g/kg (SE=1.0) on June 19 (Figure 3-6). Protein then recovered to 16.7g/kg (SE=1.0) prior to the July 2 haying operation, then decreased to a level equivalent to the previous low by July 18. Recovery to levels equivalent to those of July 2 occurred prior to application of the second haying operation on August 16, and recovered further during late summer-fall to reach 23.7g/kg (SE=1.0) by October 10.

3.3.3 Root TNC and Soluble Protein Entering Dormancy

In addition to soluble root protein, measures of root TNC were conducted in October, 1997, to provide an assessment of alfalfa response to treatments at the end of the entire growing season. Analysis of variance showed levels of root protein and TNC were not significantly different among treatments in October 1997 ($p>0.05$), but means, standard errors and sample sizes are presented for intuitive consideration (Table 3-5). Regression analysis of paired root protein and TNC observations did not identify a significant relationship between the two attributes.

Table 3-5. Least squares mean soluble protein and total nonstructural carbohydrate levels in alfalfa taproots sampled October 10, 1997, under four treatments.

	Root Protein (g/kg DM)			**Root TNC (g/kg DM)**		
Treatment	**Mean**	**Std Error**	**N**	**Mean**	**Std Error**	**N**
GZHY	20.3	1.0	20	567	10	20
HYGZ	20.6	1.0	22	534	10	18
GZGZ	22.8	1.0	21	506	12	14
HYHY	23.7	1.0	25	521	11	17

3.3.4 White Crown Bud Density

White crown bud densities adjusted for crown area, crown depth, and taproot diameter, respectively, did not differ significantly among treatments, April and October sampling dates, and treatment by sampling date interactions ($p>0.05$). Mean adjusted white bud densities by treatment for April (prior to the growing season), and October (after the growing season), 1997, are presented for intuitive consideration in Table 3-6.

Table 3-6. Least squares mean white bud density adjusted for crown area, crown depth and taproot diameter in alfalfa sampled April 21 and October 10, 1997, prior to and following four SMS treatments. Standard error of means are presented in parentheses.

	Buds/cm^2 of crown area		**Buds/cm of crown depth**		**Buds/cm of root diameter**		**Sample size**	
SMS	**4/21**	**10/10**	**4/21**	**10/10**	**4/21**	**10/10**	**4/21**	**10/10**
GZHY	2.7 (0.3)	1.7 (0.3)	3.9 (0.7)	6.5 (0.7)	8.4 (1.3)	13.4 (1.5)	22	20
HYGZ	2.0 (0.3)	1.7 (0.3)	5.1 (0.7)	4.3 (0.7)	9.8 (1.3)	8.6 (1.3)	19	22
GZGZ	2.3 (0.4)	1.8 (0.3)	5.4 (0.8)	4.4 (0.7)	10.6 (1.3)	9.2 (1.3)	15	21
HYHY	3.0 (0.3)	2.0 (0.3)	5.5 (0.7)	5.9 (0.6)	11.9 (1.3)	12.0 (1.2)	22	25
Grand mean	2.5 (0.2)	1.8 (0.2)	5.0 (0.4)	5.3 (0.3)	10.2 (0.7)	10.8 (0.6)	78	88

3.4 Discussion

3.4.1 Soluble Root Protein

This experiment focused on changes in root soluble protein through the entire growing season of 1997 under four treatments representing sward management systems (SMS). However, this experiment had a limited experimental design whereby the lack of a true control treatment prevented separation of treatment effects from natural changes in root soluble protein due to seasonal growth and other factors. Therefore, while there was some evidence both grazing and haying components within SMS induce depletion of root protein supplies, this could not be fully confirmed statistically. Practically speaking, all the SMS in this experiment are commonly employed on wapiti farms and therefore could be described as "control sward management systems" against which the other three treatments could be compared (Van Lent-Staden, personal communication, January 31, 1997[♣]). In the end, analysis of variance in root soluble protein did not identify any significant SMS main effect or SMS by sampling date interaction. Therefore, one could hypothesize SMS treatments were not sufficiently variable to generate significant differences in response, and hence, the alfalfa stand used in this experiment may have responded in a similar manner to each of the four SMS.

Root reserves of TNC and N have, for many decades, been considered important precursors for shoot regrowth following defoliation, with earlier studies emphasizing the importance of TNC (Graber et al. 1927; Smith 1962, 1964; Heichel et al. 1988), and more recent studies identifying a critical role for N reserves (Volenec et al. 1996; Avice et al. 1997; Kalengamaliro et al. 1997; Cunningham et al. 1998). Typically, soluble proteins and amino acids comprise about 60% of total N in alfalfa taproots and are the main N pools used during reinitiation of shoot growth (Barber et al. 1996; Volenec et al. 1996). Concentrations of these taproot N pools, especially in winterhardy cultivars, increase markedly near the end of the growing season and into winter hardening (Cunningham et al. 1998). Volenec et al. (1996) report increases in soluble root protein of up to 2.5 times that of late summer levels during this period, while Cunningham et al. (1998) report more modest gains of 20-50% are typical. Soluble root protein levels typically remain high through winter, then decrease markedly by up to 50% with the onset of spring growth, before being replenished after substantial shoot growth has occurred (Volenec et al. 1996).

In this experiment, declines in soluble taproot protein averaged 37% during the onset of spring growth from April 21 to May 21 across the four treatments (Table 3-4), and were consistent with results of previous studies (Volenec et al. 1996; Cunningham et al. 1998). Soluble protein declined another 13-16% by June 19 in the HYGZ and HYHY treatments where plants were not treated until July. This concurs with studies noting declines in root N concentrations of nearly 50% during the initiation of spring growth in alfalfa (Bula and Smith 1954; Hendershot and Volenec 1993a; Volenec et al. 1996; Cunningham and Volenec 1998). Root protein levels did not show replenishment until after June 19 in the

---

[♣] Beef Specialist, Animal Industry Division, Alberta Agriculture Food and Rural Development

HYGZ and HYHY treatments which is consistent with other studies reporting root N redeposition is delayed until substantial spring shoot growth has occurred (Hendershot and Volenec 1993a; Volenec et al. 1996). Another treatment-wide commonality in this experiment was the steady replenishment of root protein levels in late summer and autumn whereby soluble root protein levels rose 47% from July 18 to October 10 (Table 3-4). This is consistent with reports that marked redeposition of root N reserves occurs during autumn in alfalfa, which then remain relatively constant during winter and decline with the onset of shoot growth the following spring (Hendershot and Volenec 1993b, Li et al. 1996; Volenec et al. 1996). However, in this experiment, October 10 levels of root protein did not fully recover to the pre-growing season levels observed in April.

Three factors possibly acted solely or in combination to produce significantly lower root protein levels in October than in April. First, the management system employed on the site prior to this experiment was a one-cut haying system. Presumeably, this was a less severe defoliation treatment than any of the four SMS in this experiment. On that basis, soluble root protein levels should be higher at the start of the previous winter than in October after this experiment. Secondly, this experiment was conducted in a year when July through September precipitation was 41% of the long-term average. Thus, late summer-fall drought conditions may have restricted fall regrowth, and subsequently, root protein replenishment leading up to the killing frost on October 6. Thirdly, while soluble root protein levels are known to increase during winterhardening (Cunningham et al. 1998), soluble protein synthesis during cold hardening may continue till soil is permanently frozen, thereby effectively continuing in the absence of significant photosynthesis until soil temperatures are –1 to –2°C (McKenzie et al. 1988). Consequently, root soluble protein may have increased well beyond the killing frost (October 6) and the final sampling date (October 10), especially when the first full 24 hour period with sub-zero temperatures was not observed until October 24 (Environment Canada 1999). By that date, soluble root protein levels may have been much greater than on October 10, and as a result, may have been more similar to levels entering winter the previous year.

Concentrations of soluble proteins across SMS ranged from 12 to 30 mg of soluble protein/kg of root tissue, with the maxima occurring in April and minima during midsummer. These values fall within the ranges reported in two of three previous studies. Li et al (1996) report ranges of 10 to 63mg/kg in a study of seasonal changes in soluble root protein from September through July under a two cut haying system. Their reported maximum occurred mid-winter. Cunningham et al. (1998) report a range of 30 to 52 mg/kg in a varietal comparison study looking at soluble root protein accumulation during winterhardening from September to December in undefoliated first year alfalfa. Their reported minimum and maximum values occurred in September and December, respectively, thereby reinforcing the concept of an increasing pool of root soluble protein as winterhardening progresses. Avice et al (1996), in a trial conducting single to multiple defoliations from May to July, observed a range of 13 to 73mg/kg in plants sampled post-treatment during July and August. In summary, quantitatively, the observed range in values falls inside the range established in previous studies, though current maxima do not reach that of previous studies. This may be due to seasonal, genotype and defoliation regime differences.

In this experiment, herbaceous biomass removal in haying components of treatments HYGZ, GZHY and HYHY (two hayings) were 70, 78, 78, and 75% of available herbaceous biomass, respectively (see Appendix 10). Biomass removal in grazing components of treatments HYGZ, GZHY and GZGZ (two grazings) were 86, 56, 63 and 50% of available herbaceous biomass but were unadjusted for growth during grazing periods. Numerous studies (Hendershot and Volenec 1993b, Li et al. 1996; Volenec et al. 1996) report a defoliation-induced pattern of root protein loss followed by recovery in alfalfa after hay cutting. Those studies report hay defoliation reduces concentrations of taproot proteins, and especially amino acids, for two to three weeks following shoot removal, after which taproot N pools are rapidly replenished after substantial shoot growth. Defoliation of alfalfa results in mobilization of up to 40% of taproot total N to support shoot regrowth shortly after defoliation (Avice et al. 1996). This results in root N reserves accounting for about 90% of total N in regrowth shoots at the beginning of regrowth (day 3) versus only about 50% after 30 days when N fixation and translocation have largely recovered. Kalengamaliro et al. (1997) observed a decrease of approximately 20% of soluble root protein content over a ten day period following complete removal of above-ground biomass in 91 day old alfalfa seedlings. Kim et al. (1991) report declines of 30 to 40% in taproot total N during a two week period following complete defoliation of one year old alfalfa plants. Ourry et al. (1994) report declines up to 70% of taproot protein over a 30 day regrowth period in three month old alfalfa seedlings defoliated to a 6cm height. Volenec et al. (1996) report declines of 10 to 20% of soluble protein in taproots of completely defoliated alfalfa before replenishment is initiated, and after 24 days of regrowth 45% of the N found in regrowing leaves of alfalfa was derived from roots.

In this experiment, a loss-recovery pattern was evident after haying in the HYGZ treatment (Figure 3-4) whereby soluble protein levels decreased 37% from July 2 to 18 after haying, then increased by 23% from July 18 to 31 (albeit a statistically insignificant increase). A similar pattern was observed after the first haying component of the HYHY treatment (Figure 3-6) where soluble protein levels dropped 23% from July 2 to 18 after haying, then apparently increased 11% from July 18 to 31 (albeit a statistically insignificant increase). Those results are similar to results from previous studies by Li et al. (1996) and Volenec et al. (1996). Li et al. (1996) report a 36% decline in soluble root protein of alfalfa in the two weeks immediately following a June 2 defoliation to 5cm, then an 18% increase over the next 2 weeks. Volenec et al. (1996) report a 20% decline in root protein during the first two weeks following complete defoliation of alfalfa, then an increase of 13% over the next two weeks. I was unable to confirm the loss portion of the loss-recovery pattern after the second (August 16) hay cut in the HYHY treatment because roots were not sampled again until October (Figure 3-6). None of the SMS which employed grazing exhibited a significant loss in soluble root protein following a grazing period (Figures 3-3, 3-4, 3-5). In the GZHY treatment (Fig. 3-3), post-grazing root protein replenishment was apparent from June 19 to July 2 at 19% (albeit not significant) and coincident with a modest recovery in above-ground biomass after the June 5 to19 grazing period. In the GZGZ treatment (Figure 3-5), root protein replenishment was 71% from July 31 to August 16 following the June 5 to July 31 grazing period. In summary, root protein replenishment after wapiti removal was relatively rapid and immediate in comparison to the approximate two week drawdown in root protein levels observed following haying components in this and previous studies. Under grazing components of SMS, most plants in the stand were likely utilized to some degree early in the grazing period, and thereby initiated root N mobilization for initiation or development of buds prior to the end of the grazing period, which in turn resulted in quicker root N replenishment post-grazing than that observed following hay cuts in this experiment. As such, root N mobilization to support initiation or development of buds may have occurred prior to the end of the grazing period, thereby resulting in quicker root protein replenishment than observed following hay cuts.

Furthermore, there were at least three plausible reasons why data from this experiment suggested root protein reserves went through a post-haying loss-recovery phase while the loss portion of this phase was absent post-grazing. The first was that during grazing periods where most plants were grazed, crown buds were likely to develop beyond the white bud stage into a "ready-to-grow" green phase due to the removal of apical dominance. Conversely, prior to a hay cut, although there may have been green buds present in a "ready to grow" state, white bud initiation and development was yet to be released from apical dominance (Leach 1979; Brummer and Bouton 1991). Subsequently, the root protein drawdown in the post-haying state to initiate/develop new white buds was likely more evident than in the post-grazed state where white buds were already released from apical dominance by grazing and had proceeded through those stages of development.

A second explanation was that regrowth from axillary buds on stems defoliated by grazing may have contributed a greater portion of regrowth biomass than in hayed stands, thereby lowering the amount of regrowth from crown buds which may require more mobilized endogenous N from root protein supplies relative to axillary buds. In theory, having a greater proportion of pre-existing axillary buds in a grazed stand may be a less N-costly source of regrowth than in a hayed stand where regrowth is predominantly from crown buds (Leach 1979). However, it follows that one would expect a delay in herbaceous regrowth in a hayed stand if crown buds must be initiated or developed versus pre-existing axillary buds which have already started to grow in a grazed plant that was defoliated days or weeks before the end of the grazing period. I did not observe any such delay, therefore this explanation may be less valid than the former argument. Moreover, this explanation directly contradicts observations from the first experiment (as described in Chapter 2) in this study where the majority of regrowth biomass was crown bud-derived following both wapiti-simulated defoliation and mowing. In summary, there were likely adequate numbers of crown buds in a "ready to grow" green state in both hayed and grazed stands, and root protein draw-down was associated with conversion of white buds to the "ready to grow" green state. This conversion process was presumeably ongoing in grazed stands as individual plants were defoliated whereas it would be expected to occur at cutting in hayed stands.

A third possible explanation is based on the theory that differential residual biomass in grazed versus hayed components of SMS could affect quantities of remobilized N for regrowth. Research by Kim et al. (1991) report that, after cutting 10 week old alfalfa seedlings to a height of 6cm, 45% of remobilized endogenous N in regrowth tissue is derived from remnant leaf and stem, and in roughly equal quantities. The remaining 55%, comes from root N reserves. However, in this experiment, levels of residual biomass were largely similar among grazing/haying components of treatments (Figures 3-3 through 3-6), though the ratio of leaf to stem may have differed from grazing to haying components of SMS.

3.4.2 Root TNC

In this experiment, root TNC levels were measured in October as plants were about to enter dormancy to provide an indication of alfalfa regrowth potential in addition to root protein (Table 3-3). Mean root TNC concentrations entering dormancy ranged from 506 to 567 g/kg but were not significantly different among treatments. Those TNC levels were similar or greater than ranges previously reported as adequate for winter survival and spring initiation of growth (380-400 g/kg by Smith 1962; 461-522 g/kg by Smith et al. 1989, 300-450 g/kg by Li et al. 1996; 350-375 g/kg by Kalengamaliro et al. 1997; 505-544 g/kg by Volenec et al. 1996), and imply that the alfalfa stand had ample TNC reserves to survive winter and initiate spring growth successfully, regardless of SMS. However, this experiment was conducted in only one growing season, therefore, possible cumulative effects of employing these treatments in multiple years could lead to critical lows in TNC reserves entering dormancy.

3.4.3 White Crown Bud Density

Crown buds are normally initiated in the fall, remain dormant during winter and begin growth when environmental conditions become favorable in the spring (McKenzie et al. 1988). White crown buds are normally the most cold tolerant tissue, until they turn green, at which point they lose their cold hardiness. As such, they are generally considered to be a more important source of spring growth than green buds (Cunningham et al. 1998; McKenzie et al. 1988). In this experiment, white crown bud densities were not significantly different among treatments within April or October sampling dates (Table 3-5). The five year old stand used in this experiment withstood all four treatments and recovered ample root protein and TNC reserves during the late summer-fall recovery period to insure adequate proliferation of white buds as plants approached dormancy in October. October white bud density was equivalent to that in April, thereby providing at least an equivalent morphological potential for reinitiation of growth to that observed in spring, 1997.

The only available comparative research citing effects of treatments on crown bud densities was a study by Brummer and Bouton (1991) performed in Georgia, U.S.A, where irrigated two year old alfalfa (cv. Alfagraze) plants were clipped to a 7.5cm height every 2 weeks for 16 weeks from June to October, and resulting crown buds were counted in November. Analyzing data from that study, Brummer and Bouton observed crown bud densities of 1.5 buds/cm^{2}of crown area and 4.9 buds/cm of taproot diameter. Those densities are less than the grand means established across treatments in this experiment of 1.8 buds/cm^{2}of crown area and 10.8 buds/cm of taproot diameter in October, 1997. However, the differences between studies appear logical in that Brummer and Bouton's treatments simulated an intensive rotational grazing system with a very short rest period which could be considered more severe than treatments in this experiment and which could be expected to result in less crown bud generation due to greater stresses of defoliation.

In summary, by October 1997, the mature stand used in this experiment was adequately prepared for another growing season based on white crown bud density, root TNC and root protein levels regardless of SMS. This apparent resiliency may not apply where SMS from this study are applied to younger stands as in Brummer and Bouton's work.

3.5 Conclusions

Regardless of SMS, soluble root protein was depleted from roots during initial shoot growth in spring (pre-treatment) and accumulated steadily during late summer and autumn (post-treatment). Analysis of variance in root protein indicated no significant SMS by sampling date interaction. However, in two of three SMS which employed haying, a significant loss in root protein was observed in the approximate two week period following haying, which was then followed by recovery in root protein. This typifies a loss-recovery pattern in root protein following haying. Conversely, in the only two SMS where root protein was measured during the approximate two week period following grazing, a significant increase in root protein was evident in one treatment and a similar trend in the other. And, for two other SMS where root proteins were measured beyond two weeks post-grazing, no losses in root protein were evident. These results provide cursory evidence of direct root protein recovery following grazing and contrasts the loss-recovery pattern after haying. Differences were attributed primarily to initiation of root protein mobilization on a staggered schedule as individual plants were grazed within the grazing period versus delayed protein mobilization until post-cutting in haying components of SMS.

Root protein levels of plants, though adequate to support spring growth initiation, were significantly lower entering dormancy in October than in April under all treatments. This was presumeably due to the collective stress caused by treatments, abnormally dry weather from July through September, and a sampling date that may have preceded cessation of pre-winter soluble protein synthesis in plants. Root TNC and crown white bud densities entering dormancy in October were adequate for renewal of spring growth in all treatments. The apparent resiliency of alfalfa to the stresses of all SMS may be in part due to the well established five year stand in this experiment whereas most previous studies utilized first or second year stands.

In summary, this experiment employed treatments based on typical sward management systems (SMS) on western Canadian wapiti farms where alfalfa stands may be used for both pasture and/or hay production. Important practical conclusions were that adequate recovery periods were important to root protein recovery following the initiation of growth in spring and especially during late summer to insure critically adequate levels entering dormancy. When managing alfalfa stands for pasture or hay, a minimum recovery period of three to four weeks is recommended to allow for replenishment of soluble root protein supplies. Further, recovery periods likely need to be longer after cutting for hay than following the end of a grazing period, but this requires additional research to confirm.

3.6 References

Agriculture Canada. 1988. Soil Landscapes of Canada: Alberta. Canada Soil Inventory, Land Resource Research Centre, Research Branch, Agriculture Canada Publication 5237/B. Supply and Services Canada. 8 pp., 2 maps.

AOAC (Association of Official Analytical Chemists). 1990a. Protein (crude) in animal feed, copper sulfate/titanium dioxide mixed catalyst Kjeldahl method. 988.05 p.70. In: Official Methods of Analysis of the AOAC. Fifteenth Edition.

AOAC (Association of Official Analytical Chemists). 1990b. Fat (crude) or ether extract in animal feeds. 920.39 p.79. In: Official Methods of Analysis of the AOAC. Fifteenth Edition.

AOAC (Association of Official Analytical Chemists). 1990c. Metals in plants. 985.01. In: Official Methods of Analysis of the AOAC. Fifteenth Edition.

Avice, J.C., A. Ourry, G. Lemaire, J.J. Volenec and J. Boucaud. 1997. Root protein and vegetative storage protein are key organic nutrients for alfalfa shoot regrowth. Crop Sci. 37:1187-1193.

Avice, J.C., A. Ourry, J.J. Volenec, G. Lemaire and J. Boucaud. 1996. Defoliation-induced changes in abundance and immuno-localization of vegetative storage proteins in taproots of *Medicago sativa* L. Plant Physiol. Biochem. 34:561-570.

Barber, L.D., B.C. Joern, J.J. Volenec and S.M. Cunningham. 1996. Effects of supplemental nitrogen on alfalfa regrowth and taproot nitrogen mobilization. Crop Sci. 36:1217-1223.

Bouton, J.H., S.R. Smith, Jr., D.T. Wood, C.S. Hoveland, and E.C. Brummer. 1991. Registration of 'Alfagraze' alfalfa. Crop Sci. 31:479.

Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem. 72:248-254.

Brummer, E.C. and J.H. Bouton. 1991. Plant traits associated with grazing-tolerant alfalfa. Agron. J. 83:996-1000.

Bula, R.J. and D. Smith. 1954. Cold resistance and chemical composition in overwintering alfalfa, red clover and sweetclover. Agron. J. 46:397-401.

Cook, C.W. and J. Stubbendieck. 1986. Range research: basic problems and techniques. Soc. Range Management. Denver. Colorado. 317pp.

Cunningham, S.M. and J.J. Volenec. 1998. Seasonal carbohydrate and nitrogen metabolism in roots of contrasting alfalfa (*Medicago sativa* L.) cultivars. J. Plant Physiol. 153:220-225.

Cunningham, S.M., J.J. Volenec and L.R. Teuber. 1998. Plant survival and root and bud composition of alfalfa populations selected for contrasting fall dormancy. Crop Sci. 38:962-969.

Cyr, D.R. and J.D. Bewley. 1990. Proteins in the roots of the perennial roots of chicory (*Cichorium intybus* L.) and dandelion (*Taraxacum officinale* Weber) are associated with overwintering. Planta 182:370-374.

Environment Canada. 1993. Environment Canada Atmospheric Environment Service Canadian Climate Normals: Prairie Provinces 1961-90. Minister of Supply and Services Canada. 266pp.

Environment Canada. 1999. Environment Canada Atmospheric Environment Service Climatological Station Register at Fabyan North. July 1, 1995 to September 30, 1999. 54pp.

Fargey, P.J. 1987. Wapiti selection of grass and legumes. p. 24-26. In: Renecker, L.A. (ed.). Focus on a new industry. Proceedings of the Alberta Game Growers Association Conference 1. Red Deer, Alberta. 110pp.

Graber, L.F., N.T. Nelson, W.T. Luekel and W.B. Albert. 1927. Organic food reserves in relation to growth of alfalfa and other perennial herbaceous plants. In: Research Bulletin 80, Univ. of Wisconsion, Madison, WI.

Haigh, J.C. and R.J. Hudson. 1993. Farming wapiti and red deer. Mosby Year-Book, Inc. St. Louis, Missouri. 369 pp.

Heichel, G.H., R.H. Delaney and H.T. Cralle. 1988. Carbon assimilation, partitioning, and utilization. p. 195-228. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Heinrichs, D.H. 1963. Creeping alfalfas. Adv. Agron. 15:317-337.

Heinrichs, D.H. 1978. The future of alfalfa for pasture in dry regions and research requirements. p. 4-9. In: D.K. Barnes (ed.). Report of the 26th Alfalfa Improvement Conf., Brookings S.D. 6-8 June, 1978. USDA-ARS, St. Paul, MN.

Hendershot, K.L. and J.J. Volenec. 1993a. Taproot nitrogen accumulation and use in overwintering alfalfa (*Medicago sativa* L.). J. Plant Physiol. 141:68-74.

Hendershot, K.L. and J.J. Volenec. 1993b. Nitrogen pools in taproots of *Medicago sativa* L. after defoliation. J. Plant Physiol. 141:129-135.

Hicks, C.R. 1973. Fixed, random and mixed models. p.173-186 In: Hicks, C.R. Fundamental concepts in the design of experiments. Second edition. Holt Rinehart and Winston. New York. 349 pp.

Hudson, R.J. and J.Z. Adamczewski. 1990. Effect of supplementing summer ranges on lactation and growth of wapiti (*Cervus elaphus*). Can. J. Anim. Sci. 70:551-560.

Kalengamaliro, N.E., J.J. Volenec, S.M. Cunningham and B.C. Joern. 1997. Seedling development and deposition of starch and storage proteins in alfalfa roots. Crop Sci. 37:1194-1200.

Kim, T.H., A. Ourry, J. Boucaud and G. Lemaire. 1991. Changes in source-sink relationship for nitrogen during regrowth of lucerne (*Medicago sativa* L.) following removal of shoots. Aust. J. Plant Physiol. 18:593-602.

Kim, T.H., A. Ourry, J. Boucaud and G. Lemaire. 1993. Partitioning of nitrogen derived from N_2 fixation and reserves in nodulated *Medicago sativa* L. during regrowth. J. Exp. Bot. 266:555-562.

Klein, L. 1997. Pasture and forages for wapiti. Grazing and Pasture Technology Program Publ. GPP0397. Extension Branch, Saskatchewan Agriculture and Food. 12 pp.

Leach, G.J. 1979. Regrowth characteristics of lucerne under different systems of grazing management. Aust. J. Agric. Res. 30:445-465.

Li, R., J.J. Volenec, B.C. Joern and S.M. Cunningham. 1996. Seasonal changes in nonstructural carbohydrates, protein, and macronutrients in roots of alfalfa, red clover, sweetclover, and birdsfoot trefoil. Crop Sci. 36:617-623.

Mapfumo, E., M.A. Naeth, V.S. Baron, A.C. Dick and D.S. Chanasyk. 2002. Grazing impacts on litter and roots: perennial versus annual grasses. J. Range Manage. 55:16-22.

McKenzie, J.S., R. Paquin and S.H. Duke. 1988. Cold and heat tolerance. p. 259-302. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Ourry, A., J. Bigot and J. Boucaud. 1989. Protein mobilization from stubble and roots and proteolytic activities during post-clipping regrowth of perennial ryegrass. J. Plant Physiol. 143:298-303.

Ourry, A., T.H. Kim and J. Boucaud. 1994. Nitrogen reserve mobilization during regrowth of *Medicago sativa* L.: Relationships between their availability and regrowth yield. Plant Physiol. 105:831-837.

Province of Alberta. 1994. Livestock Industry Diversification Act and Pursuant Regulations. In: Statutes of Alberta, 1990, Chapter L-22.7 with amendments in force as of January 1, 1992. Consolidated November 17, 1994. Queen's Printer, Edmonton, Alberta.

Renecker, L.A. 1988. Wapiti farming in Canada. p. 118-140. In: Valdez, R. (ed.). Proceedings: First International Wildlife Ranching Symposium. Las Cruces, New Mexico. New Mexico State University. 321 pp.

Sheaffer, C.C., G.D. Lacefield and V.L. Marble. 1988. Defoliation schedules and stands. p. 411-438. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Smith, D. 1962. Carbohydrate reserves in alfalfa, red clover, and birdsfoot trefoil under several management schedules. Crop Sci. 2:75-78.

Smith, D. 1964. Winter injury and the survival of forage plants. Herb. Abstr. 34: 203-209.

Smith, S.R., Jr. and J.H. Bouton. 1993. Selection within alfalfa cultivars for persistence under continuous stocking. Crop Science 33:1321-1328.

Smith, S.R., Jr., J.H. Bouton and C.S. Hoveland. 1989. Alfalfa persistence and regrowth potential under continuous grazing. Agron. J. 81:960-965.

Smith, S.R., Jr., J.H. Bouton and C.S. Hoveland. 1992. Persistence of alfalfa under continuous grazing in pure stands and in mixtures with tall fescue. Crop Science 32:1259-1264.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. Sixth Edition. Iowa State University Press. Ames, Iowa. 593pp.

SPSS Inc. 1999. SYSTAT 9 Statistics I. SPSS Inc. Chicago. IL. 660 pp.

Staswick, P.E. 1994. Storage proteins of vegetative tissues. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45:303-322.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife Publication T/245. Edmonton, Alberta, Canada. 59pp., 1 map.

Teuber, L.R. and M.A. Brick. 1988. Morphology and anatomy. p. 125-162. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Thorleifson, I. 2001. Pasture mixes and management for elk. p. 77. In: The Canadian Elk and Deer Farmer Early Spring 2001. Vol. 8 No. 2. Calgary, Alberta, Canada.

Undersander, D., D.R. Mertens and N. Thiex. 1993a. Neutral detergent fibre-amylase procedure. Method 5.1. p.95-99. In: Forage analyses procedures . National Forage Testing Association. Omaha, Nebraska.

Undersander, D., D.R. Mertens and N. Thiex. 1993b. Standardizing alpha-amylase activity for neutral detergent fiber determination. Method 5.2. p.100-103. In: Forage analyses procedures . National Forage Testing Association. Omaha, Nebraska.

Volenec, J.J., A. Ourry and B.C. Joern. 1996. A role for nitrogen reserves in forage regrowth and stress tolerance. Physiol. Plant. 97:185-193.

Wolf, D.D. and V.G. Allen. 1990. Yield and regrowth characteristics of alfalfa grazed by steers during spring and summer. Agron. J. 82:1079-1082.

Wonders, W.C. 1969. Atlas of Alberta. Government of Alberta and Univ. of Alberta. Edmonton, Alberta, Canada.

4.0 FORAGING EFFICIENCY OF WAPITI ON TAME PASTURE

4.1 Introduction

In recent decades, a significant wapiti *(Cervus elaphus)* farming industry has emerged in western Canada (Nixdorf 2001) within which most farmed wapiti derive their main feed supply from tame pastures (Renecker 1988). Tame pastures for wapiti are commonly dominated by and sometimes solely comprised of legumes, usually alfalfa (*Medicago sativa* L.) (Haigh and Hudson 1993; Klein 1997; Thorleifson 2001). Feeding behavior studies which quantify foraging efficiencies of wapiti on legume pastures relative to grass-dominated stands are needed to recommend forage mixtures and grazing systems for wapiti.

Previous studies of wapiti feeding behavior in western Canada have focused on native rangelands and unimproved pastures in the Aspen Parkland, and Boreal Mixedwood ecoregions, where wapiti once roamed in abundance (Gates and Hudson 1981, 1983; Hudson and Nietfeld 1985; Hudson and Watkins 1985; Jiang and Hudson 1992, 1994). In those areas, wapiti forage extensively on grasslands interspersed among aspen boreal forest (Gates and Hudson 1981) but maximize seasonal nutrient intake by variable inclusion of browse and forbs as part of a mixed diet dominated by grasses (Gates and Hudson 1983; Hudson and Watkins 1986). Wapiti modulate bite size and rate in response to available forage biomass, sward structure and composition (Hudson and Nietfeld 1985; Jiang and Hudson 1992, 1994; Wickstrom et al. 1984). Domestic grazers vary bite size as a result of sward structural variation (Burlison et al. 1991; Laca et al. 1992), including sward height and bulk density (Laca et al. 1992; Milne et al. 1991; Barthram and Grant 1984), and consume more green than cured biomass, and more leaves than stem (Arnold 1987; Black and Kenney 1984; Dudzinski and Arnold 1973). Jiang and Hudson (1994) report similar selectivity by wapiti, observing selection on both horizontal and vertical planes within a sward, and sacrificing bite size to accomplish compensatory improvements in diet quality to maintain nutritional intake.

This experiment assessed estimated bite size, bite rate, dry matter and nutritional intake of wapiti on grass-dominated versus pure alfalfa tame pastures. The effect of available plant biomass and stand composition of tame pastures on feeding behavior was of specific interest. Bite size, bite rate, dry matter (DM) intake, protein and energy intake were dependent variables,

4.2 Materials and Methods

4.2.1 Experimental Area and Animals

The experiment was conducted at 53° 03' 30" North, 110° 51' 30" West near Vermilion, in east central Alberta, Canada. The experimental site contained loam textured Orthic Black Chernozemic soils on a morainal parent material with level to gently undulating surface expression (Agriculture Canada 1988) and was situated in the Aspen Parkland ecoregion of Alberta which has been described climatically and ecologically as a transition zone between boreal forest and grassland environments (Strong and Leggat 1992). The ecoregion is characterized by a cool, continental climate with short, warm summers and long, cold winters (Wonders 1969). Total annual precipitation for the ecoregion is normally 412mm with a median summer precipitation of 259mm where the majority of precipitation falls in June and July (Strong and Leggat 1992). Precipitation and temperature data pertaining to this experiment have been described in Chapter 3 including reference to the first killing frost of -5°C on October 6, 1997.

Pure legume pastures utilized in the experiment were two paddocks (0.25 and 0.5ha in size) on a mature stand of alfalfa (*Medicago sativa* L. cv. Alfagraze) seeded in May 1992 at 9kg/ha (inoculated with *Rhizobium meliloti*) at a 15cm row spacing and subsequently cut for hay once annually to a height of 10cm between July 1-15 from 1993 to 1996 inclusive. Fertilizer was applied in a one-time deep banding operation prior to seeding in May 1992 at a rate of 30kg N ha^{-1}, 150kg P ha^{-1}, 30kg S ha^{-1}, and 30kg K ha^{-1}. Sethoxydim and 2,4-DB were applied during the 1995 and 1996 growing season at rates of 556 and 1698g ha^{-1} a.i., respectively, to eliminate grasses and non-leguminous weeds. Prior to initiating the experiment in 1997, plant species other than alfalfa were present in the stand at a combined total of <1% of above-ground biomass. This included dandelion (*Taraxacum officinale* Weber), yarrow (*Achillea millefolium* L.), aster (*Aster spp.*), northern bedstraw (*Galium boreale* L.) and foxtail barley (*Hordeum jubatum* L.). Stand composition was determined from four randomly selected 20 x 100cm clip plots of above-ground live herbaceous biomass taken from each paddock prior to initiating grazing trials, segregated by species, dried at 60°C for 48 hrs and weighed.

Grass-dominated pastures used in the experiment were two-0.5ha paddocks containing a mature mixture of meadow bromegrass (*Bromus riparius* Rehm. cv. Regar) and alfalfa (*Medicago sativa* L. cv. Alfagraze) (seeded in 1992 at 4.5kg/ha alfalfa and 11.2kg/ha meadow bromegrass). Alfalfa ranged from 0 to less than 25% of above-ground biomass within paddocks. Some plant species other than alfalfa and meadow brome were present in the stand at levels <1% of above-ground biomass. This included smooth bromegrass (*Bromus inermis* Leyss. ssp. inermis), Kentucky bluegrass (*Poa pratensis* L.) and the species aforementioned in the alfalfa paddocks. Stand composition was determined from four randomly selected 20 x 100cm clip plots of above-ground live herbaceous biomass taken from each paddock prior to initiating grazing trials, segregated by species, dried at 60°C for 48 hrs and weighed.

Each paddock was cut to a height of 10cm for hay on either July 2 or July 31, 1997 and subsequent regrowth used as pasture in the grazing trials of this experiment. The alternate cutting dates were required due to a lack of physical resources required to replicate the experiment at the same time. As a result, grazing trials on common pasture stand types were replicated but with different grazing dates. This was not considered a large problem because data were pooled across grazing trials of a given pasture type. Grazing was initiated when mean live above-ground herbaceous biomass from four randomly selected 20 x 100cm clip plots exceeded 2500kg/ha following oven drying of samples at 60°C for 48hrs and weighing. Stands were visually uniform at this time. Initiation of grazing corresponded to the first bud stage in alfalfa and the late vegetative stage for grasses and a mean stand height exceeding 25cm.

Animals used in grazing trials were randomly selected from a base herd of 24 female wapiti born in 1996. A herd of 8 head was selected for trial 1 and 16 head for each of trials 2 to 4. Each trial herd contained at least one hand-reared animal thereby facilitating close observation. In August, 1997, prior to the experiment, the animals weighed 215 ± 8kg, while following the experiment in early October, 1997, animals weighed 232kg ± 9kg. This corresponded to a mean stocking density across the four trials of 15.7AU/ha with a range from 15.1 in August to 16.3 in October, respectively. The stocking density resulted in rapid depletion of available forage in paddocks over an eight to eleven day period in the various grazing trials.

4.2.2 Experimental Design

Four grazing trials (see Table 4-1) were employed in the experiment. Data collected from each trial was comprised of multiple randomly selected and observed and recorded foraging sequences of wapiti in a given pasture type, with observations from separate trials being pooled within each of the two pasture types for regression analysis. The logic behind trial grazing dates was to allow forage biomass to accumulate beyond 2500kg/ha, that figure being in the range of previous studies of wapiti foraging behavior (Wickstrom et al 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986). Secondly, I wanted to conduct the grazing trials prior to the first killing frost (which occurred October 6, 1997) to avoid any potential confounding effects on foraging behavior and to maximize the range over which biomass depletion by wapiti would occur.

Table 4-1. Description of 1997 grazing trials.

Trial #	Pasture type	Pre-trial haying date	Trial grazing dates
1	Alfalfa	July 2	August 3 –13
2	Grass dominated	July 2	September 4-12
3	Alfalfa	July 31	September 16-25
4	Grass dominated	July 31	September 28-October 5

Prior to initiating each grazing trial, animals were placed in an area adjacent to the trial paddock on the same pasture type for at least two weeks pre-trial, including exactly the same growth state as found in trial paddocks for three days prior to the onset of each trial. Within grazing trials, animals were selected randomly within the herd for observation of foraging parameters primarily during the dawn or dusk peak feeding periods (Gates and Hudson 1983).

4.2.3 Foraging Behavior and Available Herbaceous Biomass

Estimates of the functional response of wapiti have been calculated previously as the product of bite size and rate (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986). Foraging sequences of randomly selected individual wapiti from within the herd were recorded on video camera during normal feeding bouts between 0600 and 2100 each day using the method established by Hudson and Nietfeld (1985) and Hudson and Watkins (1986). However, data collected on August 10-11 (trial 1), September 4-5 (trial 2), September 22-23 (trial 3) and October 2 (trial 4) were lost due to the failure of video equipment. Data analyses of remaining video footage were based on 1 to 5 minute observation sessions on individual wapiti which were used to compute cropping bite rate observations and corrected to exclude time allocated to non-foraging activities. Foraging was defined as bites taken during all foraging postures described by Jiang and Hudson (1993) but excluding searching postures and grazing while lying or kneeling (due to the rarity of occurrence). Individual observation sessions ended when animals spent more than 30 seconds consecutively in non-foraging activities or when the session reached the 5 minute limit. This approach was similar to methods employed by Hudson and Watkins (1986). Immediately following each observation session, 10 simulated or mimicked "bites" were hand-picked to reproduce the plant types and parts selected by the animal observed using the method of Hudson and Nietfeld (1985) and Hudson and Watkins (1986). A bite was defined as a single cropping motion of the jaws or mouth that severed a mass of tissue from a plant (Shipley et al. 1994). Bite samples were separated into alfalfa, meadow bromegrass and other fractions, dried for 48h at 60°C and weighed. Estimated dry matter intake rates in g /minute (DMI) were calculated as the product of bite rate (bites/minute while foraging) and bite size (g/bite). I did not employ a marker method (Jiang and Hudson 1992) to estimate DMI rates for various reasons. Firstly, wapiti were not pre-conditioned to pelleted feed required for marker administration. Secondly, handling facilities were not available to facilitate separation and feeding of individual animals to initiate individual consumption of marker-laden feed, nor were all animals behaviorally conditioned for same. Further, the bite count method employed in this experiment was deemed adequate having been verified as similar in precision and bias to the marker method (Jiang and Hudson 1992).

For each wapiti observed in a foraging session, each video-recorded observation and "10 bite" sample was paired with a 20 x 100cm clip plot of above-ground available biomass harvested in the immediate proximity of where the animal foraged. These samples were separated into alfalfa, meadow brome and other fractions, dried for 48h at 60°C and weighed to estimate available forage biomass (as kg DM/ha) and stand composition within pasture types.

Live above-ground herbaceous biomass from four randomly located 20 x 100cm clip plots was harvested before and after each grazing trial. Samples were oven dried at 60°C for 48hrs and weighed. The difference between mean total available herbage supplies before and after each grazing trial was divided by the number of days and wapiti used in each trial to estimate mean daily forage removals on a per head basis.

4.2.4 Chemical Analyses and Nutritional Intake Rates

Using video and clip plot data for individual wapiti recorded in foraging sessions, common patches or "session locales" no more than 10m x 10m in area were identified where two or more wapiti were observed grazing on similar available biomass and stand composition. Subsequently, "10 bite" herbage samples from session locales were pooled and used for analyses of crude protein and digestible energy content. This reduced the cost of chemical analyses and increased the sample size available. Estimated mean DMI rates across all foraging sessions within respective "session locales" were then adjusted using crude protein and digestible energy content (from chemical analyses) as multipliers to estimate protein and energy intake of wapiti per unit time expended foraging.

Pooled "10 bite" herbage samples for "session locales" were ground in a Wiley mill to pass a 1mm sieve, then sampled separately for analysis of crude protein and digestible energy via ADF (acid detergent fiber). Crude protein was analyzed using a mixed catalyst Kjeldahl method (method 988.05, AOAC 1990a) where subsamples were digested in sulfuric acid in the presence of a copper sulfate/titanium dioxide catalyst to convert organic nitrogen to ammonium sulfate, then ammonia from steam distilling titrated with a standard acid to derive nitrogen content and a 6.25 multiplier applied to estimate crude protein. ADF was analyzed using the Ankom method (method 973.18, AOAC 1990b) where an acidified quaternary detergent solution was used to dissolve cell components, hemicellulose and soluble minerals leaving a residue of cellulose, lignin, heat-damaged protein and a portion of cell wall protein and ash. After filling and sealing Ankom filter bags with a heat sealer unit, the filter bags were submerged in the reflux vessel of an Ankom 200 Fiber Analyzer. Solution was continually forced through and around each filter bag, then ADF was determined gravimetrically as the residue remaining after extraction. Measures of ADF were then adjusted by multipliers weighted for grass and alfalfa content which were developed by Van Soest et al. (1979) for estimating digestible energy content.

4.2.5 Statistical Analyses

Regression analyses were performed for each of the two pasture types to elucidate lines of best fit using available biomass as the independent variable and estimated bite size, bite rate, DMI, crude protein intake and digestible energy intake rates of wapiti as dependent variables. Observations from separate grazing trials were pooled by pasture type prior to regression analysis. Outliers were not removed from any analysis. A variety of models including linear and nonlinear models were explored to find a best fit for the true nature of various relationships. Initially, I tested equation types including asymptotic regressions using Michaelis-Menton and logarithmic equations used in previous studies (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986; Wilmshurst 1992). Separate regressions were calculated for alfalfa and meadow bromegrass-dominated pastures to identify differences in foraging strategies employed by wapiti on grass-dominated versus alfalfa pastures. Best fit equations with probabilities <0.05 were accepted as significant and selected for presentation in the results section with the additional conservative proviso that accepted models generated a sufficiently large observed F ratio to satisfy the Box and Wetz Rule of Thumb as described by Draper and Smith (1998). That rule effectively requires the observed F for the regression to exceed the F critical value for a given test percentage point (for example, for $p<0.05$) by a factor of four in order for the regression equation to be considered useful for prediction.

4.3 Results

4.3.1 Forage Removals and Available Herbage

Foraging behavior of wapiti during peak feeding periods was observed over a wide range of available herbaceous biomass on alfalfa-only and grass-dominated stands. Wapiti were observed alternating between foraging and resting bouts during daylight hours, and on that basis, the time available for grazing was not considered a limiting constraint to wapiti consumption.

Total available herbage supplies were depleted from maxima to minima during trial grazing periods with ranges from 2840 to 310 and 2630 to 640kg/ha for alfalfa-only and grass-dominated stands, respectively. Grazing periods ranged from eight to eleven days in the various trials. Mean estimated daily forage removal attributed collectively to grazing and trampling was 7.2, 6.9, 7.9, and 7.8kg DM per head for trials 1 through 4, respectively.

Stand composition varied among pasture types. Alfalfa content consistently exceeded 99% of available biomass dry matter in the alfalfa-only pasture type. In grass-dominated pasture, alfalfa content ranged from 0 to 25% of available biomass dry matter.

4.3.2 Dry Matter Intake Rate

Estimated DMI rates under alfalfa-only and grass-dominated stands reached similar maxima near peak available biomass, but declined according to different mathematical functions at intermediate levels of available biomass (Figure 4-1). On alfalfa-only stands, intake declined sharply from a predicted intake of 23.2g/minute at a maximum observed biomass of 2840kg/ha, then remained relatively constant as available biomass declined from about 2250 to 700kg/ha. In grass-dominated stands, intake was fitted asymptotically to available biomass with a predicted intake of 18.9g/minute at a maximum observed biomass of 2630kg/ha. Between 1000 to 2000kg/ha, DMI was considerably greater on grass-dominated stands. Estimated DMI rates were a product of distinct patterns in bite size and grazing technique as stands were depleted (see 4.3.3 and 4.3.4).

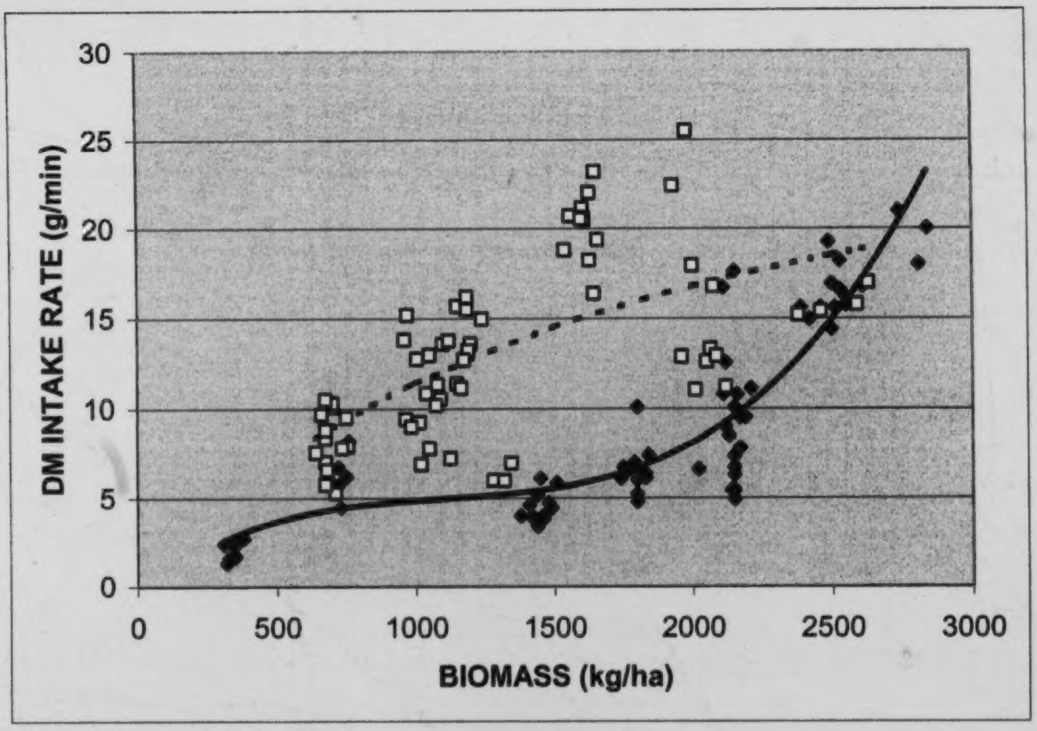


Figure 4-1. Estimated dry matter intake rate (g/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=3.15E\text{-}09X^3-1.04E\text{-}05X^2+0.0125X-0.34$, $R^2=.81$) and grass-dominated (dashed line, $Y=31.7X/(1769.8+X)$, $R^2=.41$) stands.

4.3.3 Bite Size

Estimated mean bite size was strongly correlated with available herbage under both alfalfa and grass-dominated stands, but reflected different mathematical functions (Figure 4-2). In grass-dominated stands, estimated bite size followed a predominantly linear relationship over the observed range in available biomass, but was fitted with a Michaelis-Menton equation for comparison with previous studies. At available biomass levels less than about 2250 to 2500kg/ha, mean estimated bite size was greater in grass-dominated stands than alfalfa-only stands. However, the reverse was true at or near peak available biomass levels whereby the maximum observed bite size in grass-dominated stands (0.85g/bite) was less than in alfalfa-only stands (1.05g/bite).

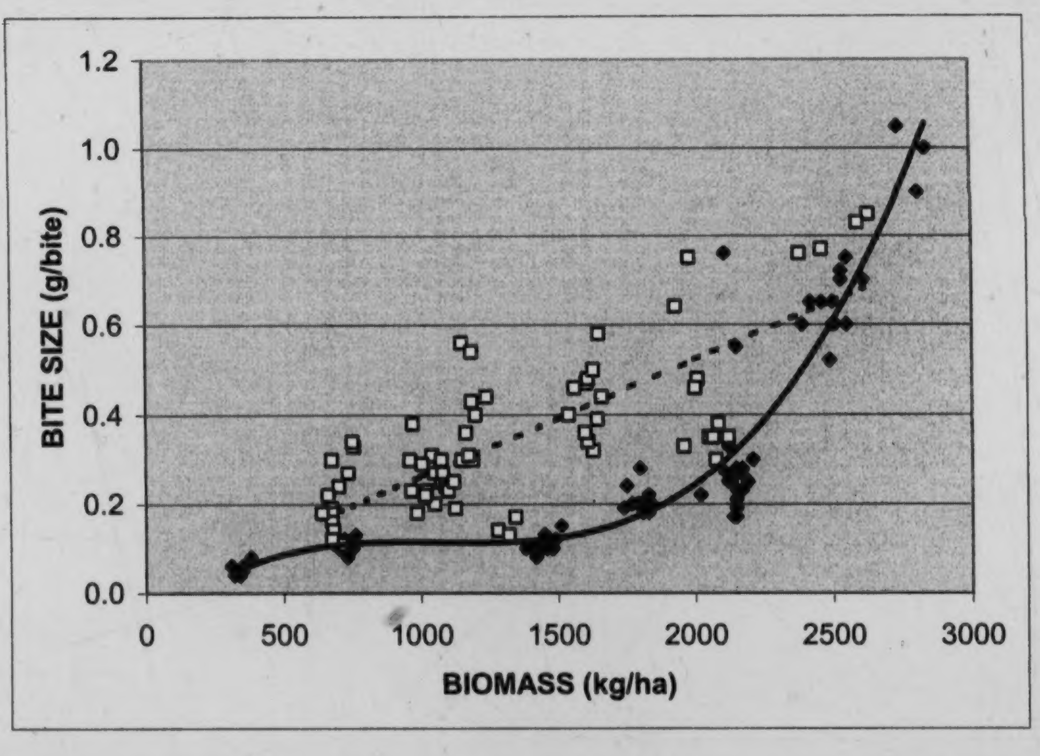


Figure 4-2. Estimated bite size (g dry matter/bite) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=1.73E\text{-}10X^3-5.57E\text{-}07X^2+5.88E\text{-}04X-0.09$, $R^2=.88$) and grass-dominated (dashed line, $Y=145.1X/(553780+X)$, $R^2=.56$) stands.

In pure alfalfa stands, estimated bite sizes exceeding 1g were observed for peak herbage supplies of about 2800kg/ha, then decreased exponentially as the stand was depleted to below about 2250kg/ha, and declined linearly to a low of 0.04g as stand biomass was depleted. I fitted a curvilinear function to this relationship after failing to fit functions used in previous studies (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986; Wilmshurst 1992). The nature of the curvilinear relationship was related to direct visual observations of distinct phases in wapiti bite prehension and ingestion behavior. This behavior can be described via four components (P1 through P4) of a third order polynomial, each representing a phase of biomass depletion in which wapiti exhibited a specific pattern of bite selection (Figure 4-3).

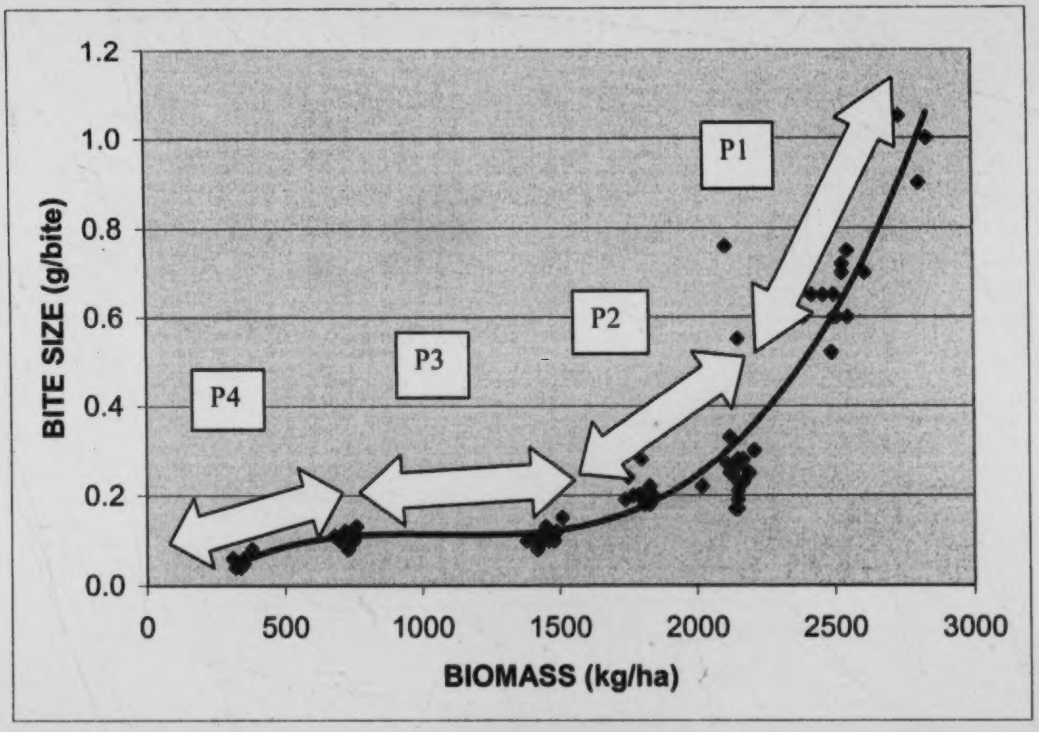


Figure 4-3. Phases of bite selection behavior by foraging wapiti in relation to estimated bite size (g dry matter/bite) and total available herbaceous biomass (kg/ha) in alfalfa-only stands.

During the first of these phases (P1), bite size declined linearly as peak biomass was depleted to about 2250kg/ha. In this P1 phase, wapiti were observed removing large bites comprised of succulent leafy plant tops and buds. Food quality was maximal during this phase with mimicked bites exhibiting mean crude protein and digestible energy contents of 28.1 ± 0.3%[♣] and 3.13 ± 0.04Mcal/kg DM, respectively. Observations during this phase concur with reports by Jiang and Hudson (1992, 1994) that wapiti maximize bite size by initially grazing the leafy tops of plants on homogeneous swards with highly digestible green material. This phase also concurs with top grazing behavior described for sheep and cattle (Milne et al. 1982, Barthram and Grant 1984).

In the second phase of depletion (P2), bite size declined as biomass was depleted from about 2250 to 1500kg/ha. During this phase, ungrazed tops of plants were relatively scarce due to prior depletion in P1, and wapiti mostly grazed leaf and axillary stem material from sides of primary stems rather than top grazing. As such, food quality of mimicked bites selected by wapiti declined from the P1 highs to P2 mean crude protein and digestible energy contents of 26.9 ± 0.7% and 3.12 ± 0.13Mcal/kg DM, respectively. Wapiti were adept at manipulating their lips and lower incisors to prehend and food along a distinct vertical plane

---

[♣] expressed as the mean ± standard error within the alfalfa stand. Jiang and Hudson (1994) report similar foraging mechanics for wapiti grazing leaves along a vertical plane, albeit on grassland rather than alfalfa.

The third phase of depletion (P3) featured a relatively stable bite size as biomass was depleted from about 1500 to less than 700kg/ha. During this phase, wapiti were observed grazing along a horizontal plane within the stand. The visual appearance of the stand during this phase was predominantly primary stems from which the majority (50-90%) of leaves and axillary stems had been removed in P2. Food quality of mimicked bites selected by wapiti declined to P3 mean crude protein and digestible energy contents of 24.0 ± 2.0% and 2.89 ± 0.07Mcal/kg DM, respectively. Wapiti were observed grazing a mixture of "mostly stem and some leaf" material in a top-down manner by the end of this phase. Grazing behavior was relatively non-selective as evidenced by some of the largest bite rate observations in the experiment over this range in available biomass.

In the final phase (P4), depletion of the alfalfa-only stand was severe and biomass levels were less than 700kg/ha. Food quality of mimicked bites selected by wapiti declined to mean crude protein and digestible energy contents of 19.0 ± 0.2% and 2.78 ± 0.08Mcal/kg DM, respectively. Wapiti were observed grazing the few remaining green leaves and stems from a harsh woody stubble of primary stems and exposed crowns. Animals were observed struggling to prehend forage while trying to avoid woody stubble which was poking their lips and muzzle, hence a decline in bite rate was apparent during this phase of bite selection.

4.3.4 Bite Rate

Bite rate was inversely related to bite size in both types of stands (Figure 4-4). Bite rate minima were associated with maximal available herbage supplies under alfalfa-only and grass-dominated stands. In alfalfa-only stands, maximal bite rate as predicted by nonlinear regression was 55 bites per minute at an available biomass level of 763kg/ha. Severe depletion of alfalfa-only stands to less than 400kg/ha available biomass resulted in a precipitous decline from bite rate maxima. In grass-dominated stands, maximal bite rate as predicted by nonlinear regression was 43 bites per minute at an available biomass level of 1250kg/ha. Declines in predicted bite rate at lower biomass levels were apparent but variability among observations was large within grass-dominated stands.

Though not shown figuratively, bite rates were negatively correlated with bite size for both alfalfa-only and grass-dominated stands. These relationships were quantified via asymptotic regression to give mathematical equations of common form where $Y = 43.47e^{-0.84X}$ (R^2=.57) for alfalfa-only stands and $Y = 54.04e^{-0.96X}$ (R^2=.41) for grass-dominated stands, where Y = bite rate in bites/minute and X = bite size in g DM/bite.

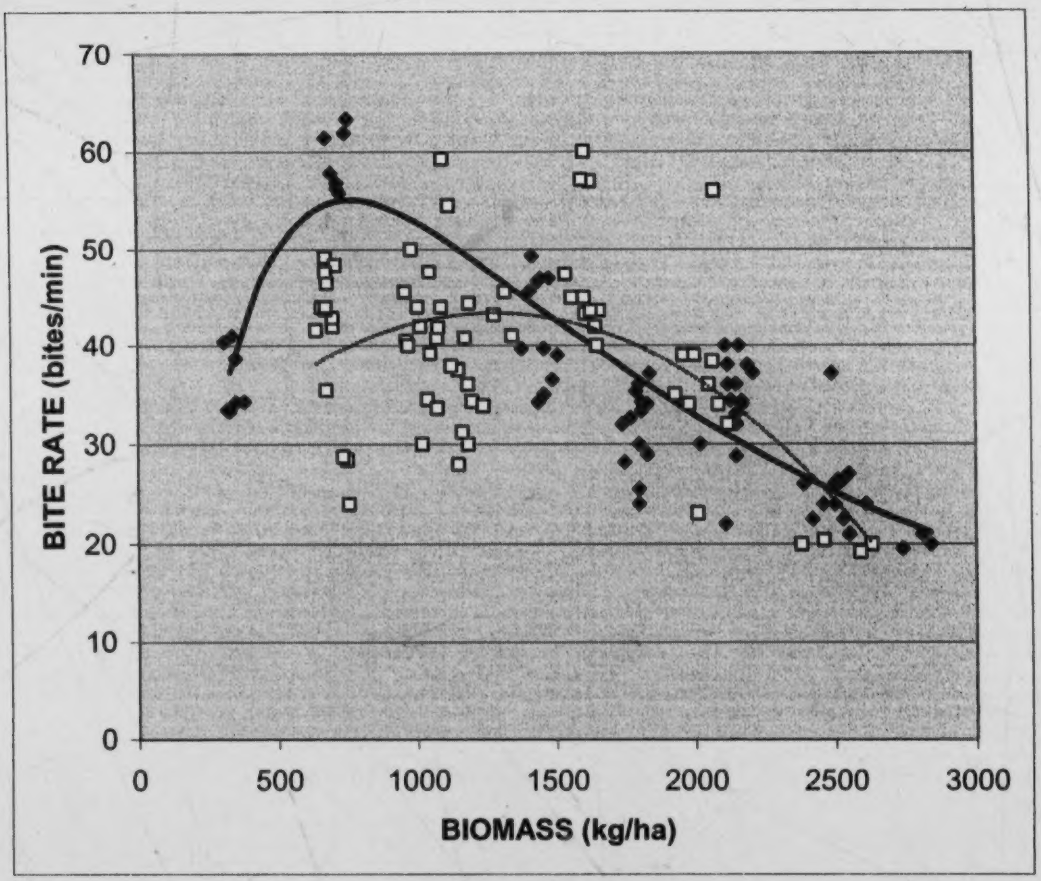


Figure 4-4. Bite rate (bites/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=55e^{(-0.5[\ln(X/762.6)/0.95]^{\wedge}2)}$, $R^2=.87$) and grass-dominated (dashed line, $Y=-1.282E\text{-}05X^2+0.033X+22.4$, $R^2=.27$) stands.

4.3.5 Nutritional Intake Rate

In alfalfa-only stands, estimated crude protein (Figure 4-5) and digestible energy (Figure 4-6) intake rates reflected the distinct curvilinear pattern previously described for DMI and bite size. For grass-dominated stands, asymptotic equations applied for crude protein (Figure 4-5) and digestible energy (Figure 4-6) intake, but were largely linear over the observed range in biomass. Estimated nutrient content of pooled mimicked bites of wapiti taken from foraging session locales were generally greater for alfalfa-only than grass-dominated stands. Crude protein content ranged from 18.8 to 28.4% and 9.5 to 15.8%, respectively, in alfalfa-only versus grass-dominated stands, with higher end values associated with the onset of grazing and declining as trials proceeded. Similarly, digestible energy content ranged from 2.72 to 3.31Mcal/kg and 2.42 to 2.75Mcal/kg, respectively, for alfalfa-only and grass-dominated stands, with higher end values associated with the onset of grazing and declining as trials proceeded. Hence, previously described differences in estimated consumption rates were magnified in the context of

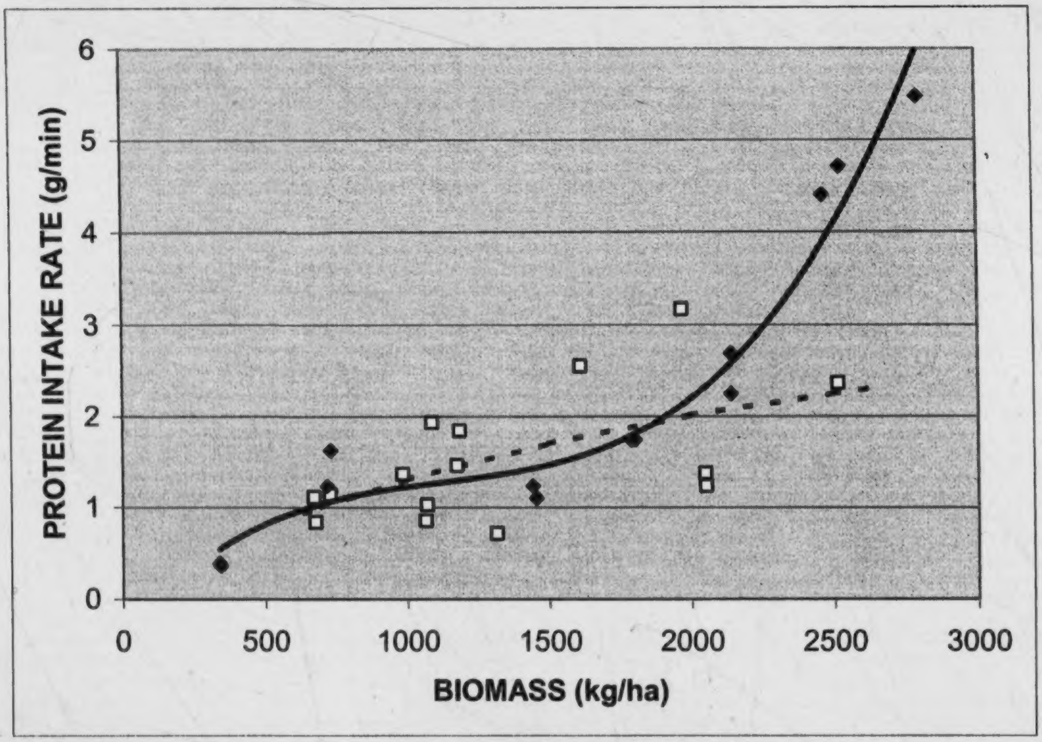


Figure 4-5. Estimated crude protein intake rate (grams/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=8.71E-10X^3-2.94E-06X^2+3.71E-03X-0.42$, $R^2=.96$) and grass-dominated (dashed line, $Y=4.39X/(2363+X)$, $R^2=.34$) stands.

nutritional intake. For available biomass levels greater than about 2000kg/ha, estimated protein intake rate was greater in alfalfa-only stands than grass-dominated stands. For available biomass levels greater than about 2500kg/ha, estimated digestible energy intake rate was greater in alfalfa-only stands than grass-dominated stands.

4.4 Discussion

4.4.1 Forage Removals and Available Herbage

A major intent of this experiment was to simulate the farm management goal of releasing animals onto high quality pasture. Therefore, grazing trials were implemented when stands were in a predominantly vegetative state and maximal available biomass levels in alfalfa-only and grass-dominated stands did not exceed 3000kg/ha. However, peak levels of available biomass were large enough to fit on the lower end of a spectrum established in previous studies where biomass exceeded 2300 (Hudson and Nietfeld 1985), 3000 (Wilmshurst 1992), 4000 (Hudson and Watkins 1986), and 7000kg/ha (Wickstrom et al. 1984). As a result, regression models in this experiment were limited to the range in

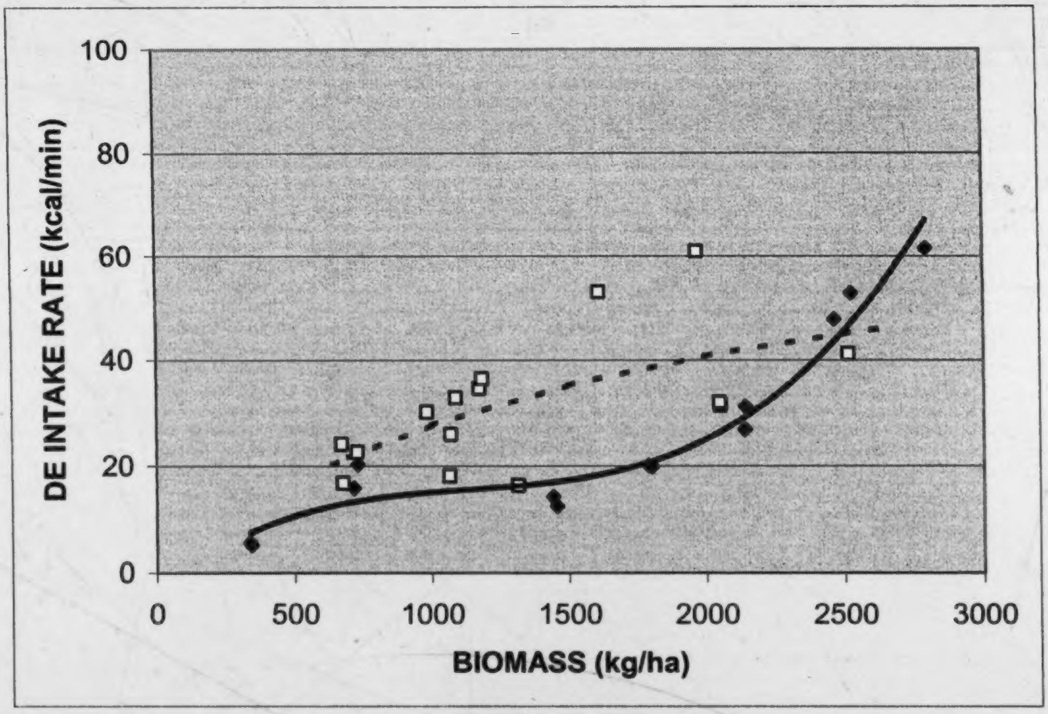


Figure 4-6. Estimated digestible energy intake rate(kcal/minute) of wapiti in relation to total available herbaceous biomass (kg/ha) in alfalfa-only (solid line, $Y=1.01E\text{-}08X^3\text{-}3.45E\text{-}05X^2+0.043X\text{-}3.47$, $R^2=.95$) and grass-dominated (dashed line, $Y=78.1X/(1825+X)$, $R^2=.39$) stands.

available biomass observed, but lend strength to management insights for pastures in a vegetative state, though during latter parts of the growing season.

Wapiti spend 30 to 60% of their daily time finding and consuming food (Gates and Hudson 1983; Wickstrom et al. 1984). In this experiment, while daily time allotted to grazing was not measured, wapiti were observed foraging intensively during the dawn and dusk peak feeding periods (Gates and Hudson 1983) and alternated between foraging and resting bouts during daylight. The latter behavior was indicative of behavior where time available for grazing was not a constraint to maximizing daily consumption (Gates and Hudson 1983). Estimated daily forage removals by grazing and trampling ranged from 6.9 to 7.8kg DM/wapiti across trials in this experiment. Those removals fit within the realm of previous studies reported at 5.7 to 6.1 (Hudson and Nietfeld 1985), 7.3 (Jiang and Hudson 1994), and 9.5kg DM/head/day (Hudson and Nietfeld 1985) for wapiti of similar body mass to this experiment.

4.4.2 Dry Matter Intake Rate

Estimated DMI rate was related asymptotically to available biomass on grassland-dominated stands and was consistent with previous studies using asymptotic or logarithmic equations to describe wapiti DMI rates on grass-dominated rangelands (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986; Wilmshurst 1992). For comparative purposes, I entered maximal available biomass levels for the grass-dominated stands (2630kg/ha) into equations derived from this and previous studies to generate a spectrum of predicted consumption rates (Table 4-2). Resultant predicted maxima from this experiment fell near the upper end of the generated spectrum and may reflect the impact of having up to 25% alfalfa content in grass-dominated stands. Unpublished data from this experiment showed alfalfa content in grass-dominated stands was positively correlated with available biomass supplies and estimated DMI. Hence, considerable dispersion among DMI rate observations in this experiment was largely attributed to variation in alfalfa content within grass-dominated stands.

For alfalfa-only stands, attempts to fit asymptotic functions used in previous studies (see Table 4-2) did not capture the true nature of the relationship. Therefore, a curvilinear function was employed and resulted in a predicted DMI maxima of 23.2g/minute at peak available biomass (2840kg/ha). This exceeds predicted consumption rates from previous studies (Table 4-2), but none of those were investigations conducted on legume-only stands. Estimated DMI results in this experiment suggest wapiti are more efficient grazers of alfalfa at available biomass levels greater than about 2500kg/ha relative to grass-dominated stands, hence the greater estimated consumption rates. However, available biomass supplies in this experiment did not reach great enough values to elicit a flattening or plateau in DMI rate as described in previous studies (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986; Wilmshurst 1992). Estimated DMI rates in this experiment were effectively a function of bite size, rate and technique as stands were depleted by grazing.

4.4.3 Bite Size

In grass-dominated stands, bite size was asymptotically related to biomass as reported in previous studies (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986; Wilmshurst 1992). Largest (0.85g/bite) and mean (0.35g/bite) bite sizes on grass-dominated stands fit within previously reported ranges in wapiti bite size on grassland (Collins et. al. 1978; Wickstrom et al. 1984; Hudson and Watkins 1986; Wilmshurst 1992). Spatial arrangement of grass swards is such that vertical biomass distribution of the sward tends to be pyramidal with leaves dominating the top stratum (Jiang and Hudson 1994) and bulk density increasing from top to bottom of the canopy (Laca et al. 1992). As a result, vertical distribution of biomass changes with progressive defoliation and wapiti are apparently able to maintain close to maximal bite size as the stand is depleted through intermediate levels of biomass, hence the relationship is asymptotic in nature (Hudson and Watkins 1986).

Table 4-2. Predicted DMI (dry matter intake rate in grams dry matter/minute) at maximum available biomass observed in grass-dominated (2630 kg/ha) and alfalfa-only (2840 kg/ha) stands based on significant regression equations from this and previous studies.

Author	Animal Type	Body weight (kgs)	Diet Type/Month(s)	Predicted DMI at maximal biomass for grass-dominated	Predicted DMI at maximal biomass for alfalfa-only
Wickstrom et al. (1984)	Two year females	143-194	Grasses only in June, July	11.6	11.8
Wickstrom et al. (1984)	Two year females	143-194	Mixed grasses, forbs, shrubs in June, July	15.4	15.5
Hudson and Nietfeld (1985)	Adult females	Not reported	Mixed grasses, forbs in August	12.9	13.4
Hudson and Watkins (1986)	Adult females	Not reported	Mixed grasses, forbs, shrubs in August	9.6	9.7
Hudson and Watkins (1986)	Adult females	Not reported	Mixed grasses, forbs, shrubs in October	18.3	18.5
Wilmshurst (1992)	Yearling females	Not reported	Mixed grasses, forbs in July, August	19.4	19.9
This study	Yearling females	207-241	Grass-dominated in September, October	18.9	
This study	Yearling females	207-241	Alfalfa-only in August, September		23.2

The same concept applies, but in reverse manner, to explain patterns in bite size for alfalfa-only stands. In alfalfa, canopy bulk density decreases moving from top of canopy downward, effectively opposite to that in grass swards (Laca et al. 1992), hence the inability of wapiti to maintain bite size as depletion of food supplies proceeded towards scarcity in this experiment. This ultimately resulted in the use of the curvilinear function to describe the relation of bite size to available biomass for alfalfa-only stands. However, the curvilinear function presented some limitations. First, it failed to generate a plateau in bite size as reported in previous studies at maximal available biomass (Wickstrom et al. 1984; Hudson and Watkins 1986). However, such a plateau would likely be realized at biomass levels greater than the maximum (2840kg/ha) encountered in this experiment. For example, available biomass supplies exceeded 4000 and 7000kg/ha in the studies by Hudson and Watkins (1986) and Wickstrom et al. (1984), respectively.

Another criticism of the curvilinear function used in this experiment was the loss (video equipment failure) of foraging behavior data for 4 of a total of 21 days observed across the two grazing trials for the alfalfa-only pasture type. This introduced bias into the regression analysis in that data points tended to be spatially bunched according to the day observed. However, this was not of great statistical concern because only the dependent member of each data pair need be random and normally distributed to make regression analysis statistically valid (Steel and Torrie 1980), though missing data pairs impart a loss in predictive power of the equation generated. Hence, the curvilinear relationship described herein can be effectively described as a best-fit model which awaits further validation by additional data collection over a broader and entire range of available biomass levels.

4.4.4 Bite Rate

Bite rate was inversely related to bite size in both types of stands and was consistent with reports from previous studies (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986). Bite rate minima occurred in association with the largest bite sizes when available herbage supplies were maximal at the beginning of grazing trials under alfalfa-only and grass-dominated stands. Bite rate maxima occurred at mid to lower levels of available biomass in both alfalfa-only stands and grass-dominated stands as opportunities for selection of larger bites of preferred foods diminished under ongoing depletion of the stands. In alfalfa-only stands, bite rate decreased dramatically at biomass less than 700kg/ha as animals encountered difficulty prehending food from the woody stubble eminating from crowns at or near the soil surface. In contrast, declines in bite rate were less extreme under severe depletion of grass-dominated stands. This was presumeably due to the more pyramidal nature, greater bulk density, and lower amounts of woody stubble found in biomass in lower portions of grass-dominated canopies relative to alfalfa-only stands (Laca et al. 1992; Jiang and Hudson 1994).

4.4.5 Nutritional Intake Rate

In this experiment, food quality served to modulate the primary effect of bite size in determining nutritional intake. Adjusting estimated consumption rates for nutritional content of forage (crude protein, digestible energy) did not alter the nature of relationships established for estimated bite size and DMI. A curvilinear relationship applied between nutritional intake and biomass in alfalfa-only stands, while in grass-dominated stands an asymptotic relationship applied and was consistent with data from Hudson and Nietfeld (1985). Wapiti were able to achieve roughly equivalent (protein) or greater (digestible energy) estimated nutritional intake rates on grass-dominated stands than alfalfa-only stands at biomass levels less than about 2000 to 2500kg/ha. This presumeably relates to the increased foraging efficiencies associated with the pyramidal nature and greater bulk density of biomass in lower portions of the canopy in a grass-dominated stand. At available biomass levels exceeding 2500kg/ha, wapiti exhibited greater nutritional intake rates on alfalfa-only stands, presumeably because of the greater density of biomass in upper portions of the herbaceous canopy relative to grass-dominated stands. Moreover, morphological differences between grasses and forbs like alfalfa are also known to affect bite size, and in turn, functional response (Shipley et al. 1994). Thus, while for this experiment, from a general perspective, both pasture types could be described as harbouring spatially concentrated patches of food for wapiti, there were distinct differences in plant morphologic geometry between grasses and alfalfa that likely influenced maximum attainable bite size. For example, alfalfa being initially grazed at the first bud stage exhibited extensive leafy and bud-filled top growth. Following prehension and biting of this plant material, wapiti were observed with large masses of plant tissue extending outside their mouths, which, presumeably exceeded the asymptotic maximal bite size established for grass-dominated swards. This fits with observations that tiller length and sward height are typically shorter in predominantly grassy habitats (Shipley et al. 1994) such that wapiti are much less likely to take bites which exceed their mouth size. This may be why maximal bite sizes were higher in alfalfa-only stands than grass-dominated stands, and why the asymptotic relationship which applied to the latter, did not hold in the former. I was unable to locate any previous studies of nutritional foraging efficiency of wapiti on pure legume versus grass-dominated stands. However, Wickstrom et al. (1984) report greater consumption rates and bite sizes in shrub-forb communities than in grassland while Collins et al. (1978) and Hudson and Watkins (1986) report higher consumption rates in grassy meadows than in adjacent forests.

4.5 Conclusions

Patterns of dry matter and nutritional intake of wapiti varied among alfalfa-only and grass-dominated stands. Estimated foraging efficiency was greater at or near peak available biomass in alfalfa-only stands than in grass-dominated stands, presumeably because of the higher density of high quality forage in the upper portions of the alfalfa-only canopy. Wapiti were able to employ a minimal cropping rate yet maximize estimated dry matter and nutritional intake, apparently by selecting large bites of high quality leafy tops and buds of alfalfa. As stand depletion proceeded and food quality declined, wapiti were forced to select smaller bites of mostly secondary stem and leaves, and foraging efficiency declined precipitously in alfalfa-only stands. In contrast, foraging efficiencies on grass-dominated stands were superior at intermediate and lower levels of available biomass. This was attributed to the pyramidal nature and greater bulk density of available biomass in lower portions of the canopy relative to alfalfa-only stands.

This experiment provided some practical implications for management of pastures for wapiti. First, if pastures are grazed below about 2000 to 2500kg/ha, it would be advisable to maintain some grasses in the stand to offset lower expected foraging efficiencies that result on otherwise pure stands of alfalfa. Secondly, if utilizing pure alfalfa for pasture, managing for maximal biomass above about 2000 to 2500kg/ha before allowing light use by wapiti would help maximize nutritional intake. Further, the ceiling in DMI on pure alfalfa pastures was not realized in this experiment and is likely greater than 2500kg/ha. As such, alfalfa-only stands are probably best managed by short duration rotational grazing or by harvesting for hay after wapiti grazing depletes biomass to less than about 2000 to 2500kg/ha. Otherwise, a mixed grass-alfalfa stand appears best suited to maximize foraging efficiency over the widest range of available herbaceous biomass, though further research is needed to assess the optimum proportion of alfalfa.

4.6 References

Agriculture Canada. 1988. Soil landscapes of Canada - Alberta. Canada Soil Inventory, Land Resource Research Centre, Research Branch, Agriculture Canada. Publ. 5237/B.

Allen, V.G. 1985. Alfalfa management for hay and pasture. p. 5-8. In: Proc. 41st Southern Pasture Improve. Conf., Raleigh, N.C. 20-22 May, 1985. USDA-ARS. U.S. Gov. Print. Office, Washington, DC

AOAC (Association of Official Analytical Chemists). 1990a. Protein (crude) in animal feed, copper sulfate/titanium dioxide mixed catalyst Kjeldahl method. 988.05 p.70. In: Official Methods of Analysis of the AOAC. Fifteenth Edition.

AOAC (Association of Official Analytical Chemists). 1990b. Fibre (acid detergent) and lignin in animal feed. 973.18 p.82-83. In: Official Methods of Analysis of the AOAC. Fifteenth Edition.

Arnold, G.W. 1987. Influence of biomass, botanical composition and sward height of annual pastures on foraging behavior by sheep. J. Appl. Ecol. 24:759-772.

Barthram, G.T. and S.A. Grant. 1984. Defoliation of ryegrass-dominated swards by sheep. Grass Forage Sci. 39:211-219.

Black, J.L. and P.A. Kenney. 1984. Factors affecting diet selection of sheep. II. Height and density of pasture. Aust. J. Agr. Res. 35:565-578.

Burlison, A.J., J. Hodgson and A.W. Illius. 1991. Sward canopy structure and bite dimensions and bite weight of grazing sheep. Grass Forage Sci. 46:29-38.

Collins, W.B., P.J. Urness and D.D. Austin. Elk diets and activities on different lodgepole pin habitat segments. J. Wildl. Manage. 42(4):799-810.

Draper, N.R. and H. Smith. 1998. On worthwhile regressions, big F's, and R^2. p. 243-246. In: Draper, N.R. and H. Smith. 1998. Applied Regression Analysis, 3rd edition. John Wiley and Sons, Inc. Toronto. 706 pp.

Dudzinski, M.L. and G.W. Arnold. 1973. Comparisons of diets of sheep and cattle grazing together on sown pasture on the southern tablelands of new south Wales by components analysis. Austr.J. Agr. Res. 24:899-912.

Gates, C.C. and R.J. Hudson. 1981. Habitat selection by wapiti in a boreal forest enclosure. Naturaliste Can. (Rev. Ecol. Syst.) 108:153-166.

Gates, C.C. and R.J. Hudson. 1983. Forage behaviour of wapiti in a boreal forest enclosure. Naturaliste Can. (Rev. Ecol. Syst.) 110:197-206.

Haigh, J.C. and R.J. Hudson. 1993. Farming wapiti and red deer. Mosby Year-Book, Inc. St. Louis, Missouri. 369 pp.

Hudson, R.J. and M.T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. J. Range Manage. 38:80-82.

Hudson, R.J. and W.G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. Can. J. Zool. 64:1705-08.

Jiang, Z. and R.J. Hudson. 1992. Estimating forage intake and energy requirements of free-ranging wapiti (*Cervus elaphus*). Can. J. Zool. 70:675-679.

Jiang, Z. and R.J. Hudson. 1993. Foraging postures of wapiti (*Cervus elaphus*). Appl. Anim. Behav. Sci. 36:275-287.

Jiang, Z. and R.J. Hudson. 1994. Bite characteristics of wapiti (*Cervus elaphus*) in seasonal *Bromus-Poa* swards. J. Range Manage. 47:127-132.

Klein, L. 1997. Pasture and forages for wapiti. Grazing and Pasture Technology Program Publ. GPP0397. Extension Branch, Saskatchewan Agriculture and Food. 12 pp.

Laca, E.A., E.D. Ungar, N. Seligman and M.W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science 47:91-102.

Milne, J.A., J. Hodgson, R. Thompson, W.G. Souter and G.T. Barthram. 1982. The diet ingested by sheep grazing swards differing in white clover and perennial ryegrass content. Grass Forage Sci. 37:209-218.

Nixdorf, R. 2001. Specialized livestock inventory and prices update May 10, 2001 [monograph online]. Available from: Rnixdorf@agr.gov.sk.ca . Sustainable Production Branch, Saskatchewan Agriculture and Food. Accessed 2001 May 19.

Renecker, L.A. 1988. Wapiti farming in Canada. p. 118-140. In: Valdez, R. (ed.). Proceedings: First International Wildlife Ranching Symposium. Las Cruces, New Mexico. New Mexico State University. 321 pp.

Shipley, L.A., J.E. Gross, D.E. Spalinger, N.T. Hobbs and B.A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. Am. Nat. 143:1055-1082.

Steel, R.G.D. and J.H. Torrie. 1980. Correlation and Regression. p.277-278. In: Steel, R.G.D. and J.H. Torrie. Principles and Procedures of Statistics: A Biometrical Approach. Second Edition. McGraw-Hill Inc. New York. 633pp.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife. Edmonton. Alberta. Publ. T/245. 59pp.

Thorleifson, I. 2001. Pasture mixes and management for elk. p. 77. In: The Canadian Elk and Deer Farmer Early Spring 2001. Vol. 8 No. 2. Calgary, Alberta, Canada.

Van Soest, P.J., J. Fadel and C.J. Sniffen. 1979. Discount factors for energy and protein in ruminant feeds. p.63-68. In: Proc. Cornell Nutr. Conf. Cornell Univ., Ithaca, N.Y. 125pp.

Wickstrom, M.L., C.T. Robbins, T.A. Hanley, D.E. Spalinger and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48(4):1285-1301.

Wilmshurst, J.F. 1992. Forage quality and patch choice by wapiti (*Cervus elaphus*). M.Sc. thesis. Univ. of Guelph. 88pp.

Wonders, W.C. 1969. Atlas of Alberta. Government of Alberta and University of Alberta, Edmonton, Alberta, Canada.

5.0 SUMMARY DISCUSSION AND CONCLUSIONS

5.1 Experiments Performed

This study focused on various attributes of alfalfa, the most common pasture legume on western Canadian wapiti farms. Three experiments investigated morphological and physiological factors controlling regrowth in alfalfa including wapiti-simulated grazing, mowing, sward management systems, and the nutritional ecology of wapiti on tame pastures. The first experiment studied differential defoliation of alfalfa by mowing and simulated wapiti grazing and subsequent effects on regrowth and total stand morphology. The second experiment studied the morphological and physiological response of alfalfa subjected to sward management systems comprised of combinations of wapiti grazing and/or haying. The third experiment focused on factors affecting estimated dry matter and nutritional intake of wapiti while grazing alfalfa or grass-dominated tame pastures.

5.2 Main Findings and Practical Implications

In the first experiment, alfalfa proved very adaptable in regrowth response to variation in wapiti-simulated grazing and mowing at different heights of defoliation. The majority of regrowth biomass was crown-derived regardless of treatment, but axillary-derived regrowth was an important secondary source of biomass. Defoliation at taller rather than shorter heights, and stripping rather than mowing plants, resulted in quicker recovery to a harvestable stand. However, stripped alfalfa exhibited less regrowth biomass and total forage yield than mowed alfalfa. I hypothesized greater secondary stem density to result from stripping relative to mowing, but this was not apparent. Based on a review of the literature, I believe that substantial secondary stem regrowth from post-treatment crown-derived stems in mowed alfalfa may have offset any increase in secondary stem density due to stripping, but I was unable to confirm this due to limitations in methodology. Post-treatment standing forage quality was lower in stripped than mowed treatments and at taller defoliation heights. This effect on forage quality was apparently due to residual and relatively mature primary stem material being carried through to harvest after treatment application.

The results of the first experiment were largely congruent with previous studies comparing defoliation by mowing versus grazing whereby mowing resulted in greater regrowth biomass (Leach 1968, 1979; Sheaffer et al. 1988), higher quality post-treatment biomass (Leach 1970b; Kalu and Fick 1983; Wilman and Altimimi 1984), and greater overall biomass production than wapiti-simulated grazing. While wapiti-simulated grazing resulted in plants with fewer crown-derived stems than mowed plants, biomass in the post-treatment stand was still predominantly crown-derived (Leach 1970a; Wolf and Blaser 1981; Sheaffer et al. 1988). While the resultant wapiti diet might be expected to be of the highest possible food quality based on stripping of mainly leafy material, the residual biomass contributed to lower subsequent forage quality. Hence, graziers may be advised to consider alternating grazing with haying to remove woody stems and promote fresh regrowth from the crown. This recommendation is particularly advisable in view of other results in the present study (see Chapter 4) which showed a dramatic decline in foraging efficiency as wapiti made the transition from top grazing (stage P1) to using predominantly axillary leaf and stem (stage P2) as an alfalfa stand was depleted. Mowing following grazing should help maintain a stand where a stemmy coarse stubble is minimized and affords greater foraging efficiency for wapiti.

The second experiment in this study applied typical SMS (sward management systems) on western Canadian wapiti farms, where alfalfa stands may be used alternately as sources of pasture and hay. The experiment focused on insights into the effects of forage/pasture management decisions on physiological factors controlling regrowth including soluble root protein. Regardless of SMS, soluble root protein was depleted from roots during initial shoot growth in spring (pre-treatment) and accumulated steadily during late summer and autumn (post-treatment). Analysis of variance in soluble root protein did not identify a significant SMS by sampling date interaction, hence no significant differences in soluble root protein were apparent among SMS at various sampling dates. However, I found some evidence to suggest a loss-recovery pattern in root protein levels following the haying components of SMS. This was in contrast to evidence of a more immediate recovery pattern in root protein following wapiti grazing. These differences could be attributed to continual root protein mobilization during the grazing period, whereas this happened synchronously at cutting under haying components. Root protein levels of plants, though adequate to support spring growth initiation, were significantly lower entering dormancy in October than in April under all treatments. This was presumeably due to a sampling date that may have preceded the end to pre-winter soluble protein synthesis in plants, the collective stress caused by all treatments, and dry weather from July through September. Nevertheless, root TNC and crown white bud densities entering dormancy in October were deemed adequate for renewal of spring growth in all treatments.

The second experiment showed spring initiation of growth depleted soluble root proteins, adequate recovery periods were important to soluble root protein recovery, and a late summer-fall recovery period was critical to ensure adequate levels entering winter. These results concur with previous studies (Hendershot and Volenec 1993a, 1993b; Li et al. 1996; Volenec et al. 1996; Cunningham and Volenec 1998; Cunningham et al. 1998) and also suggest that root protein reserves went through a post-haying loss-recovery phase while the loss portion was not as obvious or severe following a period of grazing. Because of this, I speculate the recovery of the stand following grazing may be quicker than for mowed plants, though forage quality is likely to be lower due to more ungrazed stem carryover than in hayed stands. These results were consistent with observations in the first experiment where wapiti-simulated stripping resulted in plants exhibiting shorter recovery periods to reach a harvestable state than mowed plants. This concurs with previous studies (Li et al. 1996; Volenec et al. 1996; Kalengamiliro et al. 1997; Cunningham and Volenec 1998) indicating that when managing alfalfa stands for pasture or hay, a minimum recovery period of three to four weeks should be provided to replenish the majority of soluble root protein supplies prior to future harvests or dormancy.

In the third experiment, patterns of dry matter and nutritional intake of wapiti varied among alfalfa-only and grass-dominated stands. Foraging efficiency as measured through estimated dry matter, crude protein and digestible energy intake rates was greater in alfalfa-only stands than in grass-dominated stands at available biomass levels exceeding about 2000 to 2500kg/ha depending on which of the three dependent variables was of interest (Figures 4-1, 4-4, 4-5). This was presumeably due to a relatively higher density of high quality forage in the upper portions of the alfalfa-only canopy relative to grass-dominated stands (Laca et al. 1992; Jiang and Hudson 1994). Wapiti were able to employ a minimal cropping rate yet maximize estimated dry matter and nutritional intake by selecting large bites of leafy tops and buds of alfalfa. As alfalfa stands were depleted, wapiti were forced to select smaller bites of mostly secondary stem and leaves, and estimated foraging efficiency declined precipitously in alfalfa-only stands during this phase. Estimated nutritional and dry matter foraging efficiencies on grass-dominated stands were roughly equivalent (protein) or superior (dry matter, digestible energy) at intermediate and lower levels of available biomass. I attributed this primarily to the presumed greater bulk density of available biomass in lower portions of the grass-dominated canopy relative to alfalfa-only stands.

In summary, this experiment revealed an asymptotic pattern of DMI on grass-dominated stands similar to that reported in previous studies (Wickstrom et al. 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986; Wilmshurst 1992), but which did not apply for pure alfalfa stands (Figure 5-1). Results indicate wapiti exhibit greater foraging efficiency on alfalfa-only stands than in grass-dominated stands at available biomass levels greater than about 2000 to 2500kg/ha, and the reverse was true at lower biomass levels. The broad implications to graziers managing wapiti is that it may be advisable to maintain some grasses in the stand to offset the lower expected foraging efficiencies if stands are to be grazed to depletion below about 2000kg/ha. Secondly, if utilizing pure alfalfa stands for pasture, managing the stand to grow biomass supplies above about 2000 to 2500kg/ha before allowing light use by wapiti will help maximize wapiti nutritional intake. Although the ceiling in DMI on pure alfalfa pastures was not fitted mathematically in this experiment, it is likely greater than 2500kg/ha based on the nature of the relationship investigated. As such, pure alfalfa pastures are probably best managed by short duration rotational grazing or harvesting for hay after wapiti grazing depletes the pure alfalfa stand to levels below about 2000 to 2500kg/ha. Otherwise, a mixed grass-alfalfa stand appears best suited to maximize foraging efficiency over the widest range of available herbaceous biomass.

5.3 Overall Conclusions

In this study, alfalfa was highly adapted to regrow from both crown-derived and axillary-derived stems following defoliation by grazing or mowing, though most production resulted from crown buds. Mowing resulted in greater regrowth biomass and higher quality post-cut biomass than in a stripped stand, primarily due to less residual biomass containing woody stubble. Spring initiation of growth was depletive of root proteins, as were the collective stresses of haying, grazing and dry weather, and adequate recovery periods were important to root protein recovery, especially during the late summer-fall recovery period. Wapiti maximized estimated foraging efficiency on pure alfalfa stands

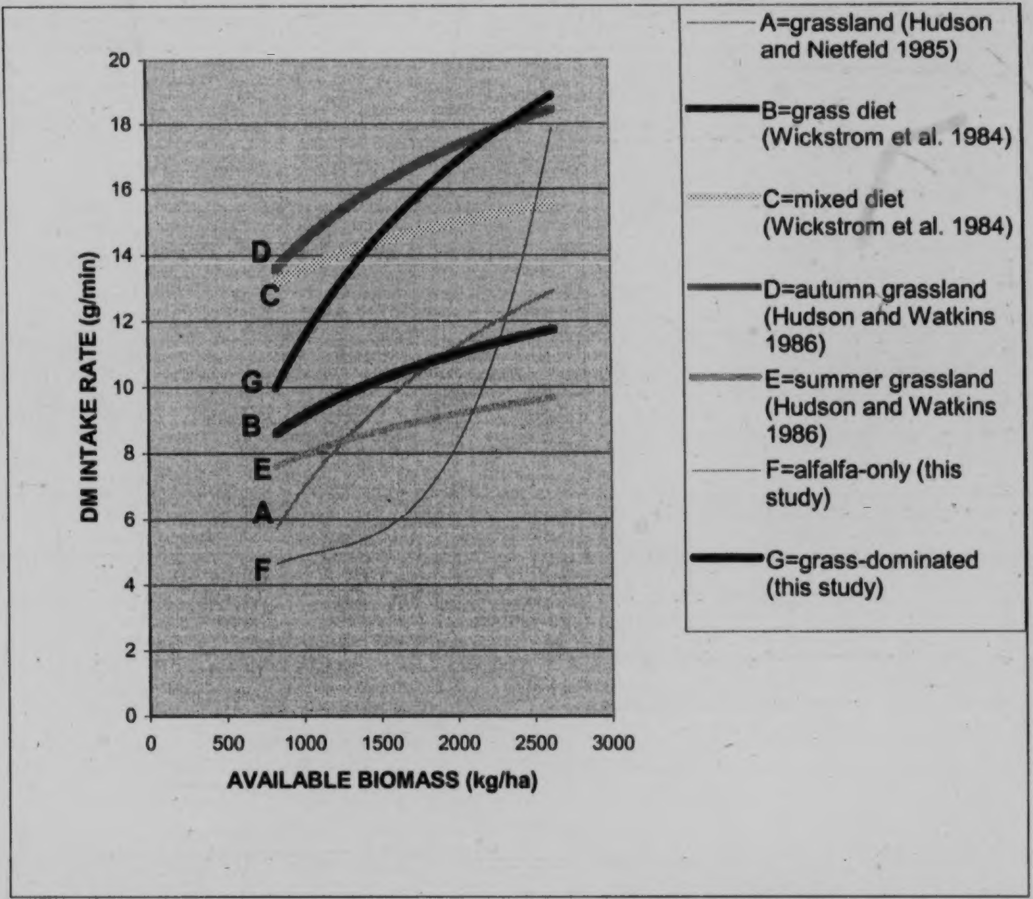


Figure 5-1. Relationships of estimated wapiti dry matter intake rate (grams/minute) and available herbaceous biomass (kg/ha) as described in this and other studies.

at or near peak biomass but as these stands were depleted wapiti were able to maintain equal or greater foraging efficiency on grass-dominated stands. Therefore, managers of tame pastures where wapiti graze heavily should consider the use of a grass:alfalfa mixture to maximize foraging efficiency and diet quality over the range of available biomass encountered. Or, if managing pure stands of alfalfa, managers should plan for short durational grazing to benefit wapiti, but be prepared to alternate this with hay cutting to foster high quality regrowth. Optimal combinations of grass to alfalfa are not yet well defined and are dependent on management decisions including targeted levels of stand depletion and whether lands are to be used for pasture alone or pasture plus hay production. Future research might also focus on leader-follower grazing systems as an alternative to haying alfalfa after wapiti grazing, or selection of alfalfa genotypes which optimize the functional response of wapiti.

5.4 References

Cunningham, S.M. and J.J. Volenec. 1998. Seasonal carbohydrate and nitrogen metabolism in roots of contrasting alfalfa (*Medicago sativa* L.) cultivars. J. Plant Physiol. 153:220-225.

Cunningham, S.M., J.J. Volenec and L.R. Teuber. 1998. Plant survival and root and bud composition of alfalfa populations selected for contrasting fall dormancy. Crop Sci. 38:962-969.

Hendershot, K.L. and J.J. Volenec. 1993a. Taproot nitrogen accumulation and use in overwintering alfalfa (*Medicago sativa* L.). J. Plant Physiol. 141:68-74.

Hendershot, K.L. and J.J. Volenec. 1993b. Nitrogen pools in taproots of *Medicago sativa* L. after defoliation. J. Plant Physiol. 141:129-135.

Hudson, R.J. and M.T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. J. Range Manage. 38:80-82.

Hudson, R.J. and W.G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. Can. J. Zool. 64:1705-08.

Jiang, Z. and R.J. Hudson. 1994. Bite characteristics of wapiti (*Cervus elaphus*) in seasonal *Bromus-Poa* swards. J. Range Manage. 47:127-132.

Kalengamaliro, N.E., J.J. Volenec, S.M. Cunningham and B.C. Joern. 1997. Seedling development and deposition of starch and storage proteins in alfalfa roots. Crop Sci. 37:1194-1200.

Kalu, B.A. and G.W. Fick. 1983. Morphological stages of development as a predictor of alfalfa herbage quality. Crop Sci. 23:1167-1172.

Laca, E.A., E.D. Ungar, N. Seligman and M.W. Demment. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science 47:91-102.

Leach, G.J. 1968. The growth of the lucerne plant after defoliation: the effect of defoliation at different stages of maturity and at different intensities. Aust. J. Agric. Res. 19:517-530.

Leach, G.J. 1970a. Shoot growth on lucerne plants cut at different heights. Aust. J. Agric. Res. 21:583-591.

Leach, G.J. 1970b. Yield and chemical composition of leaves and stems of alfalfa at intervals up the shoots. J. Agric. Food Chem. 18:652-656.

Leach, G.J. 1979. Regrowth characteristics of lucerne under different systems of grazing management. Aust. J. Agric. Res. 30:445-465.

Li, R., J.J. Volenec, B.C. Joern and S.M. Cunningham. 1996. Seasonal changes in nonstructural carbohydrates, protein, and macronutrients in roots of alfalfa, red clover, sweetclover, and birdsfoot trefoil. Crop Sci. 36:617-623.

Sheaffer, C.C., G.D. Lacefield and V.L. Marble. 1988. Defoliation schedules and stands. p. 411-438. In: Hanson, A.A., D.K. Barnes and R.R. Hill, Jr. (ed.'s). Alfalfa and alfalfa improvement. Agronomy Monograph No. 29. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc. Madison, Wisconsin.

Volenec, J.J., A. Ourry and B.C. Joern. 1996. A role for nitrogen reserves in forage regrowth and stress tolerance. Physiol. Plant. 97:185-193.

Wickstrom, M.L., C.T. Robbins, T.A. Hanley, D.E. Spalinger and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48(4):1285-1301.

Wilman, David and M.A.K. Altimimi. 1984. The in-vitro digestibility and chemical composition of plant parts in white clover, red clover and Lucerne during primary growth. J. Sci. Food Agric. 35: 133-138.

Wilmshurst, J.F. 1992. Forage quality and patch choice by wapiti (*Cervus elaphus*). M.Sc. thesis. Univ. of Guelph. 88pp.

Wolf, D.D. and R.E. Blaser. 1981. Flexible alfalfa management: early spring utilization. Crop Sci. 21:90-93.

6.0 APPENDICES

6.1 Appendix 1:

Random survey of 50 wapiti farms in Alberta in 1993 where total fenced acres were separated into native or tame pasture on a proportional basis for each farm.

farm	proportion native	proportion tame
1	0.25	0.75
2	0.00	1.00
3	0.00	1.00
4	0.30	0.70
5	0.20	0.80
6	0.00	1.00
7	0.67	0.33
8	0.33	0.67
9	0.00	1.00
10	0.50	0.50
11	0.25	0.75
12	0.54	0.46
13	0.67	0.33
14	0.40	0.60
15	0.25	0.75
16	0.71	0.29
17	0.78	0.22
18	0.18	0.82
19	0.00	1.00
20	0.41	0.59
21	0.40	0.60
22	0.44	0.56
23	0.71	0.29
24	0.20	0.80
25	0.57	0.43
26	0.29	0.71
27	0.71	0.29
28	0.42	0.58
29	0.00	1.00
30	0.67	0.33
31	1.00	0.00
32	0.40	0.60
33	0.33	0.67
34	0.00	1.00
35	0.38	0.62
36	0.56	0.44
37	0.33	0.67
38	0.66	0.34
39	0.30	0.70
40	0.92	0.08
41	0.14	0.86
42	0.20	0.80
43	0.20	0.80
44	0.01	0.99
45	0.44	0.56
46	0.19	0.81
47	0.00	1.00
48	0.80	0.20
49	0.00	1.00
50	0.02	0.98

6.2 Appendix 2:

Analysis of variance in the number of days regrowth required to reach a harvestable stand for alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-4.**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	51.56	5			
Defoliation Technique	186.78	1	186.78	65.66	.000
Replicate x Defoliation Technique	14.22	5	2.84		
Height	574.39	2	287.19	34.35	.000
Replicate x Height	83.61	10	8.36		
Defoliation Technique x Height	1.39	2	0.69	0.09	.912
Rep x Defoliation Technique x Height	74.61	10	7.46		

6.3 Appendix 3:

Analysis of variance in post-treatment herbaceous regrowth biomass (g DM/cm^2 crown area) of alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-5.**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	0.29	5			
Defoliation Technique	0.21	1	0.21	12.72	.016
Replicate x Defoliation Technique	0.08	5	0.02		
Height	0.06	2	0.03	0.86	.451
Replicate x Height	0.34	10	0.03		
Defoliation Technique x Height	0.01	2	0.005	0.41	.672
Rep x Defoliation Technique x Height	0.13	10	0.01		

6.4 Appendix 4:

Analysis of variance in total pre and post-treatment herbaceous biomass production (g DM/cm^2 crown area) of alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-6.**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	0.33	5			
Defoliation Technique	0.93	1	0.93	67.2	.000
Replicate x Defoliation Technique	0.07	5	0.01		
Height	0.46	2	0.23	5.99	.020
Replicate x Height	0.38	10	0.04		
Defoliation Technique x Height	0.05	2	0.03	1.92	.197
Rep x Defoliation Technique x Height	0.14	10	0.01		

6.5 Appendix 5:

Analysis of variance in the mean density of primary (crown-derived) stems (n/cm^2 of crown area) of post-treatment alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-7:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	2.42	5			
Defoliation Technique	1.39	1	1.39	7.63	.040
Replicate x Defoliation Technique	0.91	5	0.18		
Height	0.87	2	0.43	1.20	.341
Replicate x Height	3.61	10	0.36		
Defoliation Technique x Height	0.44	2	0.22	1.02	.393
Rep x Defoliation Technique x Height	2.13	10	0.21		

6.6 Appendix 6:

Analysis of variance in the mean density of secondary (axillary-derived) stems (n/cm^2 of crown area) of post-treatment alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-7:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	3.27	5			
Defoliation Technique	0.05	1	0.05	0.69	.443
Replicate x Defoliation Technique	0.36	5	0.07		
Height	3.35	2	1.67	2.51	.131
Replicate x Height	6.68	10	0.67		
Defoliation Technique x Height	4.37	2	2.18	4.29	.045
Rep x Defoliation Technique x Height	5.09	10	0.51		

6.7 Appendix 7:

Analysis of variance in the mean height of secondary stem origin above the root crown zone of alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-8:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	186.68	5			
Defoliation Technique	2199.76	1	2199.76	28.49	.003
Replicate x Defoliation Technique	385.98	5	77.20		
Height	5801.72	2	2900.86	51.05	.000
Replicate x Height	568.23	10	56.82		
Defoliation Technique x Height	485.31	2	242.66	5.95	.020
Rep x Defoliation Technique x Height	407.88	10	40.79		
Error	21815.02	1187			

6.8 Appendix 8:

Analysis of variance in crude protein content (g/100g) of post-treatment herbaceous biomass of alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-9:**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	4.85	5			
Defoliation Technique	19.51	1	19.51	6.71	.049
Replicate x Defoliation Technique	14.54	5	2.91		
Height	65.69	2	32.84	16.44	.001
Replicate x Height	19.98	10	2.00		
Defoliation Technique x Height	15.13	2	7.56	3.16	.086
Rep x Defoliation Technique x Height	23.91	10	2.39		

6.9 Appendix 9:

Analysis of variance in neutral detergent fibre content (g/100g) of post-treatment herbaceous biomass of alfalfa subjected to a 2x3 factorial arrangement of defoliation technique and defoliation height across 6 replicates as per the experimental design and methods described in Chapter 2.2 and **results described in Table 2-9:**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	33.65	5			
Defoliation Technique	75.11	1	75.11	9.02	.030
Replicate x Defoliation Technique	41.66	5	8.33		
Height	50.95	2	25.48	2.83	.106
Replicate x Height	90.16	10	9.02		
Defoliation Technique x Height	53.17	2	26.59	3.09	.090
Rep x Defoliation Technique x Height	86.17	10	8.62		

6.10 Appendix 10:

Herbaceous biomass removed during haying and grazing components of treatments employed in 1997 based on difference in estimates of least squares mean available biomass for start and end dates of haying and grazing components of respective treatments as described in Table 3-3 (SE = standard error N = sample size).

Treatment	Component	Start Biomass (kg/ha±SE)	N	End Biomass ♣ (kg/ha±SE)	N	Biomass Removed (kg/ha)	Biomass Removed (%)
GZHY	Grazed June 5-19	2706±135	8	381±135	8	2325	86
	Hayed July 31	2800±135	8	850±135	8	1950	70
HYGZ	Hayed July 2	4038±135	8	900±135	8	3138	78
	Grazed July 31-August 16	2125±135	8	863±135	8	1262	56
GZGZ	Grazed June 5-July 31	2831±135	8	1056±135	8	1775	63
	Grazed August 16-31	1925±135	8	982±135	8	943	50
HYHY	Hayed July 2	4175±135	8	931±135	8	3244	78
	Hayed August 16	3463±135	8	869	8	2594	75

♣ End Biomass estimates do not include any estimate of growth which may have occurred during grazing periods.

6.11 Appendix 11:

Analysis of variance in available herbaceous biomass (kg/ha) of alfalfa subjected to a randomized complete block with four treatments and fourteen sampling dates across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Figures 3-3 to 3-6:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	67.73	1			
Treatment	1900070.00	3	6335656.64	104.78	.002
Replicate x Treatment	181404.85	3	60468.28		
Sampling Date	25383600.00	13	1952580.00	342.03	.000
Replicate x Sampling Date	742136.95	13	57087.46		
Treatment x Sampling Date	23806200.00	39	6104145.46	37.48	.000
Replicate x Treatment x Sampling Date	6351293.11	39	162853.67		
Error	4689880.00	322			

6.12 Appendix 12:

Analysis of variance in root soluble protein content (g/kg) of alfalfa subjected to a randomized complete block with four treatments and eight sampling dates across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Table 3-4 and Figures 3-3 to 3-6:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	86.51	1			
Treatment	239.44	3	79.82	2.19	.268
Replicate x Treatment	109.43	3	36.48		
Sampling Date	15664.47	7	2237.78	41.85	.000
Replicate x Sampling Date	374.26	7	53.47		
Treatment x Sampling Date	1162.88	21	55.38	1.02	.481
Replicate x Treatment x Sampling Date	1139.16	21	54.25		
Error	13182.49	606			

6.13 Appendix 13:

Analysis of variance in October root soluble protein content (g/kg) of alfalfa subjected to a randomized complete block with four treatments across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Table 3-5:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	61.68	1			
Treatment	183.80	3	61.26	0.23	.870
Replicate x Treatment	796.09	3	265.36		
Error	2495.20	80			

6.14 Appendix 14:

Analysis of variance in October root TNC content (g/kg) of alfalfa subjected to a randomized complete block with four treatments across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Table 3-5:**

Source of Variation	Sum of Squares	df	Mean Square	F ratio	P
Replicate	0.01	1			
Treatment	3895.45	3	1298.48	3.21	.182
Replicate x Treatment	1212.67	3	404.42		
Error	14122.01	80			

6.15 Appendix 15:

Analysis of variance in white crown bud density per unit crown area (n buds/cm^2 crown area) of alfalfa sampled April and October under a randomized complete block with four treatments across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Table 3-6:**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	0.05	1			
Treatment	9.34	3	3.11	4.82	.115
Replicate x Treatment	1.94	3	0.65		
Sampling Date	18.77	1	18.77	3.21	.324
Replicate x Sampling Date	5.84	1	5.84		
Treatment x Sampling Date	3.96	3	1.32	0.21	.886
Replicate x Treatment x Sampling Date	19.16	3	6.39		
Error	332.91	150			

6.16 Appendix 16:

Analysis of variance in white crown bud density per unit crown depth (n buds/cm crown depth) of alfalfa sampled April and October under a randomized complete block with four treatments across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Table 3-6:**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	3.04	1			
Treatment	23.00	3	7.67	0.27	.846
Replicate x Treatment	85.97	3	28.67		
Sampling Date	3.92	1	3.92	5.71	.252
Replicate x Sampling Date	0.69	1	0.69		
Treatment x Sampling Date	80.32	3	26.77	1.48	.378
Replicate x Treatment x Sampling Date	54.36	3	18.12		
Error	1452.59	150			

6.17 Appendix 17:

Analysis of variance in white crown bud density per unit root diameter (n buds/cm taproot crown diameter) of alfalfa sampled April and October under a randomized complete block with four treatments across two replicates as per the experimental design and methods described in Chapter 3.2 and **results described in Table 3-6:**

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Replicate	0.18	1			
Treatment	183.54	3	61.18	0.74	.593
Replicate x Treatment	246.68	3	82.23		
Sampling Date	16.19	1	16.19	1.17	.475
Replicate x Sampling Date	13.83	1	13.83		
Treatment x Sampling Date	275.52	3	91.84	1.19	.446
Replicate x Treatment x Sampling Date	232.11	3	77.37		
Error	5147.38	150			